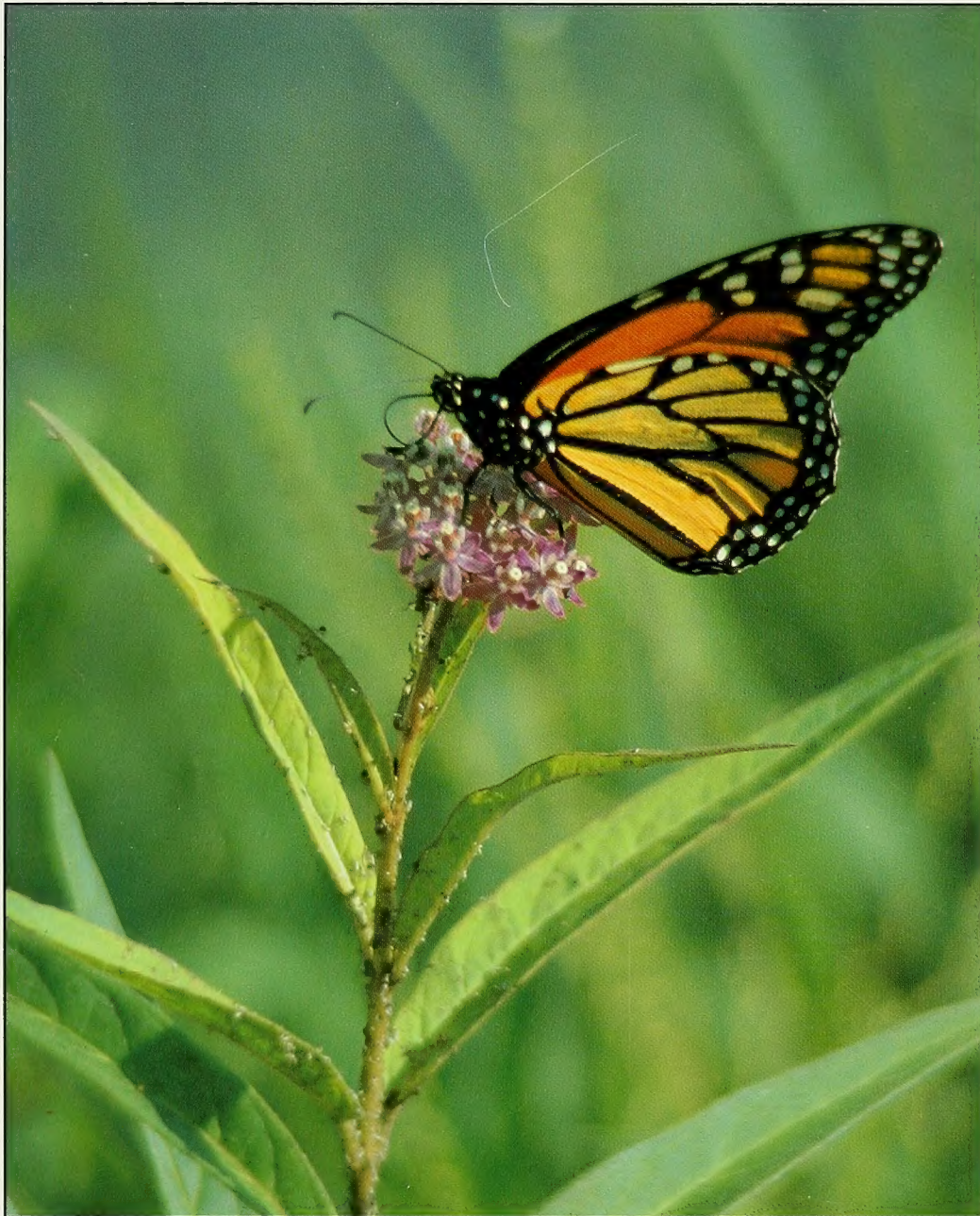


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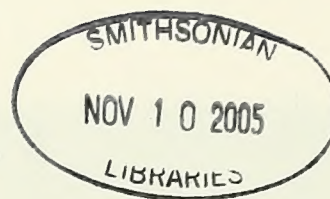
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Cover illustration: Monarch, *Danaus plexippus* (Linnaeus), and milkweed aphids, feeding on Swamp Milkweed, *Asclepias incarnata* L., September, 2005, central Illinois, USA. Photo by Peg Toliver



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SOME EUCOSMINI (TORTRICIDAE) ASSOCIATED WITH *EUCOSMA EMACIATANA* (WALSINGHAM) AND *EUCOSMA TOTANA* KEARFOTT; FOUR NEW SPECIES, A NEW COMBINATION, AND A NEW SYNONYM

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ABSTRACT. *Eucosma emaciatana* (Walsingham) is transferred to *Pelochrista* Lederer, and *Pelochrista perpropinqua* (Heinrich) is recognized as a junior synonym of *P. emaciatana*. Three species considered by previous authors to be superficially similar to *emaciatana* are reviewed: *Eucosma larana* (Walsingham), *Eucosma totana* Kearfott and *Pelochrista popana* (Kearfott). Four previously unrecognized species are described: *Eucosma piperata*, new species, *Eucosma nordini*, new species, *Eucosma taosana*, new species, and *Pelochrista powelli*, new species. Lectotypes are designated for *emaciatana* and *larana*. Adults and genitalia of these species are illustrated, and new distributional records are presented.

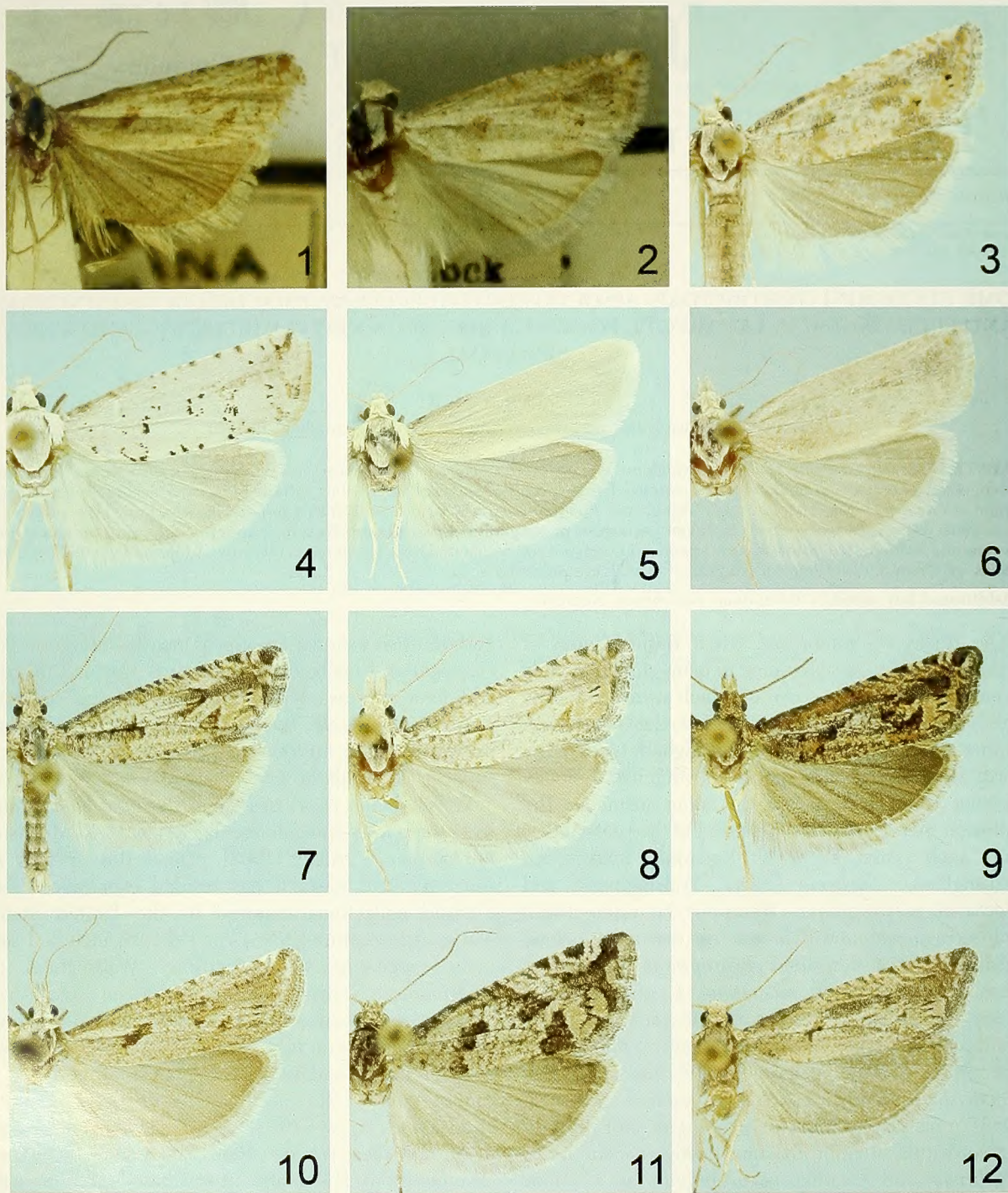
Additional key words: Oletreutinae, *Pelochrista*, Nearctic.

The Rocky Mountain and Great Basin regions of western United States are home to many similar looking species of Eucosmini, some of which were named by Walsingham in the last quarter of the nineteenth century. Lacking access to the Walsingham types, early North American tortricid specialists often had difficulty applying those names, and in some instances the confusion that resulted has persisted to the present day. One such case involves *Eucosma emaciatana* (Walsingham), *Eucosma larana* (Walsingham), and *Pelochrista perpropinqua* (Heinrich). Heinrich (1923) confused *emaciatana* with *larana* (see discussion below) and later (1929) described *perpropinqua* based on a series of specimens of *emaciatana*. I confirmed that *emaciatana* and *perpropinqua* refer to a single taxon by examining the types. Based on male genitalia, the appropriate generic assignment for this species is *Pelochrista* Lederer, a conclusion reached by Powell (1983) in his placement of *perpropinqua*, so I propose to resolve this situation by transferring *emaciatana* to *Pelochrista* and treating *perpropinqua* as a junior synonym.

In examining specimens from various institutional and private collections I encountered two previously unrecognized species of *Eucosma* Hübner that have been confused with *larana*. They are described below as *E. piperata*, new species, and *E. nordini*, new species. Also included are reviews of *E. totana* Kearfott and *P. popana* (Kearfott), two species considered by previous

authors to be similar in appearance to *larana* and/or *emaciatana*. Finally, descriptions are provided for two additional new taxa, *Eucosma taosana*, new species, and *Pelochrista powelli*, new species. The former has previously been misidentified as *totana*; the latter is superficially similar to *totana* and *taosana*.

Walsingham (1884) described *Paedisca emaciatana* from three male specimens collected by H. K. Morrison in Arizona. Fernald [1903] placed this species in *Eucosma*, and there it has resided ever since. The Fernald collection, acquired by the United States National Museum (USNM) in 1924–25, included two male specimens determined by Walsingham as *emaciatana*. Neither has an abdomen. One was collected by Morrison in Arizona in 1883 and agrees with the description of *emaciatana*, the other is lacking collection data and is in such poor condition that I cannot confirm the accuracy of its determination. Heinrich's review (1923) of *emaciatana* makes no mention of these two specimens, so I assume he did not examine them. His treatment was based on a series of specimens from Utah, and he illustrated the genitalia (Fig. 193) of a male collected by Tom Spalding at Eureka, Utah, on 27 July 1911. I examined that specimen and a number of other USNM specimens determined by Heinrich as *emaciatana* and concluded (see discussion below) that they represent *E. larana*. This explains why Heinrich, when presented with specimens of *emaciatana* collected in Arizona by O. C.



FIGS. 1-12. 1, *P. emaciatana*, lectotype male. 2, *E. larana*, lectotype male. 3, *E. larana*, male, Albany Co., Wyoming. 4, *E. piperata*, male, Oneida Co., Idaho. 5, *E. nordini*, holotype male. 6, *E. larana*, female, Oneida Co., Idaho. 7, *E. totana*, male, Grand Co., Colorado. 8, *E. totana*, male, Oneida Co., Idaho. 9, *E. taosana*, holotype male. 10, *P. emaciatana*, male, Cochise Co., Arizona. 11, *P. popana*, male, Larimer Co., Colorado. 12, *P. powelli*, holotype male.

Poling, interpreted them as representing a new species, which he described (1929) as *E. perpropinqua*.

Walsingham (1879) described *E. larana* from three specimens (2 ♂, 1 ♀) collected in Siskiyou County, California. The forewing (Fig. 2) of the lectotype (designated below) is white with pale brownish-orange markings; that of the female paralectotype is white with a few black specks and only a hint of brownish-orange markings. The specimens misidentified by Heinrich as *emaciatana* have pale yellowish-white forewings that are generously overlaid with pale brownish-orange coloration. They also have brownish-gray markings (as in Fig. 3). Specimens I collected in southeastern Idaho (Fig. 6) have very pale yellowish-white forewings with just a trace of brownish-orange coloration. I found no substantial differences in the male and female genitalia of these various specimens, and lacking any distinguishing biological information, I concluded that they all represent a single variable species. Curiously, Heinrich (1923) did correctly identify the male that he illustrated (Fig. 197) as *larana*. Two of the new species described below are similar to *larana* in forewing color, and each is sympatric with *larana* in at least a portion of the latter species' range: *piperata* in Utah and southeastern Idaho, *nordini* in southeastern Wyoming.

Kearfott (1907) reported a type series for *totana* consisting of five specimens collected by Tom Spalding and O. C. Poling in Stockton, Utah, and South Utah, respectively. The American Museum of Natural History (AMNH) has a male collected in So. Utah labeled LECTOTYPE, a designation Klots (1942) attributed to Heinrich (1923). I assume from Kearfott's remarks that the collector was Poling, but there is no such indication on the pin labels. I located four Spalding specimens from Stockton, Utah, that are likely to be the other syntypes. Only one is actually *totana*, a male in the USNM with no capture date. Both it and the lectotype bear the handwritten label "*Eucosma totana* Cotype Kearf." and Kearfott's printed red label "TYPE Collection of W. D. Kearfott". A female in the AMNH collected VIII-4-4 and bearing the red Kearfott "TYPE" label is no doubt the specimen referred to by Klots (1942) as a paralectotype, but its genitalia indicates it is not *totana*. The remaining two, a USNM specimen dated VIII-30-4 and an AMNH specimen dated VIII-1-4, are conspecific with a series of USNM specimens determined by Heinrich as *totana* but bearing a hand written label with the notation "dark var." They agree with specimens I collected in New Mexico that are sufficiently distinct in maculation and genitalic details to justify separate species status. Although I was unable to locate females of this taxon, the likelihood of it being confused with *totana* prompted me to describe it here

as *E. taosana*. This investigation also brought to my attention the previously unrecognized *P. powelli*, which can be confused with *totana* and *taosana*.

Finally, Kearfott (1907) based his description of *popana* on 27 syntypes collected by Tom Spalding at Stockton, Utah, with capture dates between 1 June and 8 August. Klots (1942) reported thirteen specimens in the AMNH as belonging to the type series, including one labeled LECTOTYPE. The lectotype designation should be credited to Klots (1942), even though he attributes it to Heinrich (1923). I examined this material and found the lectotype to be a female, rather than a male as stated by Klots. I believe nine of the other twelve specimens are *popana*, but one has a capture date of 9 August, which is inconsistent with Kearfott's remarks. Of the remaining three, two are males of *Epiblema sosana* (Kearfott), and one is a female of uncertain identity. Listed below as paralectotypes are the eight AMNH *popana* specimens whose capture dates agree with Kearfott's statements and seven USNM specimens that I judge to belong to the *popana* type series.

I am designating lectotypes for *emaciatana* and *larana* and have attached designation labels to those specimens. The specimens chosen for this purpose were originally selected by Obraztsov, but his designations were never published.

MATERIALS AND METHODS

This study is based on 607 adult specimens and 111 associated genitalia preparations. I examined the types of the five previously described species. Material was borrowed from the following institutional and private collections: AMNH, George J. Balogh (GJB), Canadian National Collection (CNC), Colorado State University (CSU), Essig Museum of Entomology (EME), Clifford D. Ferris (CDF), Los Angeles County Museum of Natural History (LACM), Museum of Comparative Zoology (MCZ), John S. Nordin (JSN), The Natural History Museum, London (BMNH), USNM, Donald J. Wright (DJW), and University of Wyoming (UWY). The line drawings were based on images generated by a Ken-A-Vision microprojector (Model X1000-1), and each associated scale bar represents 0.5 mm. Images of the genitalia of the lectotypes of *larana* and *emaciatana* were obtained by scanning negatives of photographs taken by Obraztsov of slides he had prepared. All measurements were estimated to the nearest tenth of a millimeter with the aid of a reticule mounted in a Leica MZ95 stereomicroscope. Ratios of measurements were rounded to two decimal places. Forewing length (FWL) indicates the distance from base to apex, including fringe. Aspect ratio (AR) refers to the ratio of FWL to

forewing width, the latter quantity being measured midway between base and apex. In males, the ratio of forewing costal fold length to FWL is denoted by CFR (costal fold ratio), and the ratio of valval neck width to width of basal portion of valva by NR (neck ratio). Reported values of AR, CFR and NR are averages of such values calculated for a small sample of specimens. The number of items supporting a particular statistic is indicated by n.

Some species discussed here only vaguely display the putative, ancestral, fasciate forewing pattern for the Tortricidae discussed by Brown and Powell (1991) and Baixeras (2002), but their terminology is used when possible in the forewing descriptions.

SPECIES ACCOUNTS

Eucosma larana (Walsingham)

(Figs. 2, 3, 6, 14, 15, 25, 36)

Paedisca larana Walsingham 1879:43.

Eucosma larana: Fernald [1903]:456; Barnes and McDunnough 1917:169; Heinrich 1923:110; McDunnough 1939:47; Powell 1983:34.

Eucosma emaciatana: (not Walsingham 1884) Heinrich 1923:108; McDunnough 1939:46; Powell 1983:34.

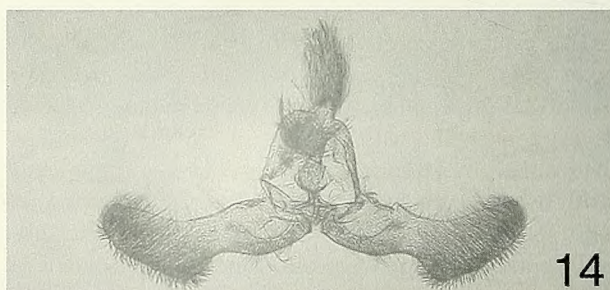
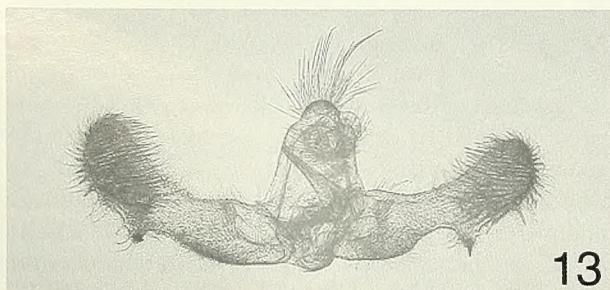
Types. Lectotype here designated (Figs. 2, 14): ♂, Sheep Rock, Siskiyou Co., California, Walsingham, 3 Sept. 1871, genitalia slide 11502, BMNH. Paralectotypes: same data as lectotype (1 ♂, 1 ♀, ♀ genitalia slide 11759, BMNH).

Diagnosis. Darkly marked specimens of *larana* can be recognized by forewing pattern (Fig. 3), but pale specimens (Fig. 6) might be confused with *nordini* or *piperata*. The forewing of *nordini* (Fig. 5) is pale yellowish white, has a gray streak on the costal fold, and shows no indication of brownish-orange mottling. The combination of white forewing color, black speckling, and brown costal marks distinguishes *piperata* (Fig. 4). One can also separate *larana*, *piperata*, and *nordini* by the shapes of the sterigmata (Figs. 36, 35, 31) and by

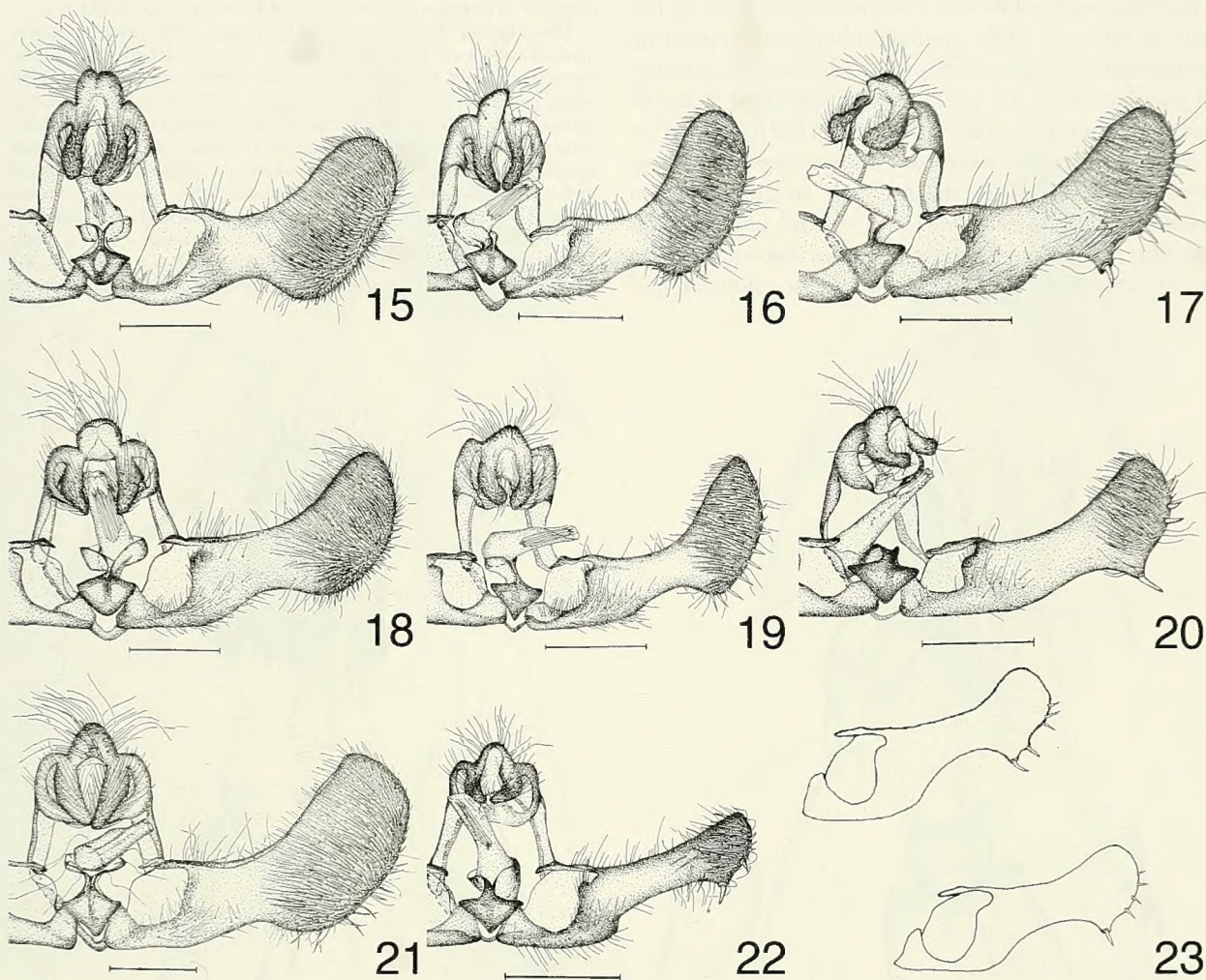
subtle but consistent differences in valval shape (Figs. 15, 18, 21).

Description. **Head:** Very pale yellowish white, long scales of upper frons and vertex often with pale gray shading preceding whiter apices; labial palpus with pale-gray lateral surface, third segment enclosed by long narrow scales of second segment; antenna yellowish white. **Thorax:** Dorsal and ventral surfaces concolorous with head, legs yellowish white to pale yellowish brown. **Forewing** (Figs. 2, 3, 6): ♂ FWL 8.5-12 mm (mean = 10.5, n = 13), AR = 3.16, CFR = 0.3, ♀ FWL 8.5-11.1 mm (mean = 10, n = 10), AR = 3.05; costa nearly straight, apex mildly acute, termen straight; dorsal surface white to pale yellowish white and variably overlaid with pale brownish-orange mottling, darker specimens with four brownish-gray marks, the first a triangular pretornal mark on dorsum, often with a few black scales at its anterior extremity, the second a subbasal mark on fold that is usually connected to dorsum by brownish-orange scaling, the third at distal end of cell, often divided longitudinally by a brownish-orange streak, the fourth anterior to ocellus; ocellus obscure, variably overlaid with brownish-orange scales and crossed longitudinally by up to four black dashes; distal one-half of costa with four, obscure, paired, white strigulae; male costal fold usually grayer than adjacent portion of wing, fringe white to yellowish white, with gray shading near apex and brownish-orange suffusion near tornus. **Hindwing:** Uniformly pale brownish gray with lighter fringe. **Male genitalia** (Fig. 14, 15): Uncus divided medially into two variably developed setose lobes with convex lateral margins; dorsolateral shoulders of tegumen well developed, often rounded and hunched, sometimes with angular corners; socii long, flat, and densely setose; vesica with 2-7 deciduous cornuti (n = 10); valva with costal margin concave, apex and ventral angle evenly rounded, distal margin very weakly convex, ventral invagination moderate, NR = 0.61, cucullus of nearly uniform width, medial surface densely setose, sacculus sparsely setose, margin of basal opening with patch of short slender spines. **Female genitalia** (Fig. 25): Papillae anales facing ventrolaterally and densely setose, medial margins very weakly sinuate, surfaces finely ridged transversely, long setae on lateral margins curving ventrally, remaining setae shorter with hooked apices; tergum VIII sparsely setose; lamella antevaginalis (Fig. 36) ringlike and weakly sclerotized, lamella postvaginalis with semitriangular posterolateral corners; membrane between sterigma and ventral extremities of tergum VIII setose; sternum VII with posterior margin approximate to sterigma and roundly invaginated to depth of one-half length of sterigma; ductus bursae strongly constricted anterior to ostium, widening anteriorly; corpus bursae with large signum near juncture with ductus bursae and small spike-shaped signum on opposite wall.

Distribution and biology. I examined 53 specimens (40 ♂, 13 ♀) from the following states and counties: CALIFORNIA: Siskiyou, Tulare; IDAHO: Oneida; UTAH: Juab; WYOMING: Albany. The flight period extends from early July to the beginning of September, and capture sites range in elevation from 5000' to 8000'.



FIGS. 13-14. Genitalia of lectotypes. 13, *P. emaciatana*, slide BMNH 11571. 14, *E. larana*, slide BMNH 11502.



FIGS. 15-23. Male genitalia. 15, *E. larana*, slide DJW 763. 16, *E. totana*, slide DJW 1022. 17, *P. emaciatana*, slide DJW 952. 18, *E. piperata*, slide DJW 762. 19, *E. taosana*, slide DJW 1035. 20, *P. popana*, slide DJW 1068. 21, *E. nordini*, slide DJW 760. 22, *P. powelli*, slide DJW 1027. 23, *P. powelli*, slides DJW 1032 and 705

This moth has been collected in open sage brush habitat in Idaho and Wyoming. No larval host has been reported.

Comments. The variation in forewing color appears to have a geographic component. Specimens from northern California and southeastern Idaho have very pale yellowish-white forewings with pale to nearly obsolescent brownish-orange markings, those from Wyoming tend to be darker, with brownish-gray markings and extensive brownish-orange mottling, and those from Utah and central California appear to be intermediate. The medial division of the uncus varies from an inconspicuous line to the pronounced indentation illustrated in Figure 15.

Eucosma totana Kearfott
(Figs. 7, 8, 16, 28, 32)

Eucosma totana Kearfott 1907:32; Barnes and McDunnough 1917:169; Heinrich 1923:108; McDunnough 1939:46; Powell 1983:34.

Eucosma spodias: Meyrick 1912:35.

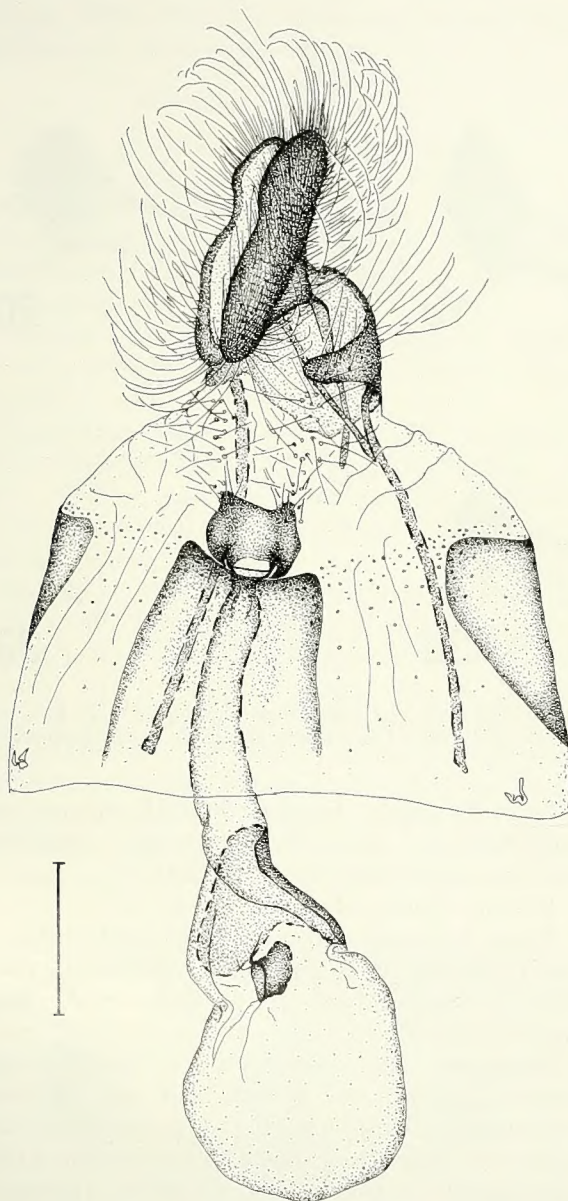
Types. Lectotype designated by Heinrich (1923): ♂, South Utah, July 1900, genitalia slide CH, 2 Dec 1919, AMNH. Paralectotype ♂: Stockton, Utah, Tom Spalding, USNM.

Diagnosis. This species can be confused with *taosana*, *popana* and *powelli*, but the following combination of dark brown forewing markings usually suffices for diagnosis: a subbasal mark on fold, a thin line along fold from subbasal mark to tornus, a pretornal triangular mark based on fold, and a chevron shaped mark at distal end of cell. Some specimens do not show the line on the fold. Superficially, *totana* is most similar to *taosana* (Fig. 9), but the latter species does not have

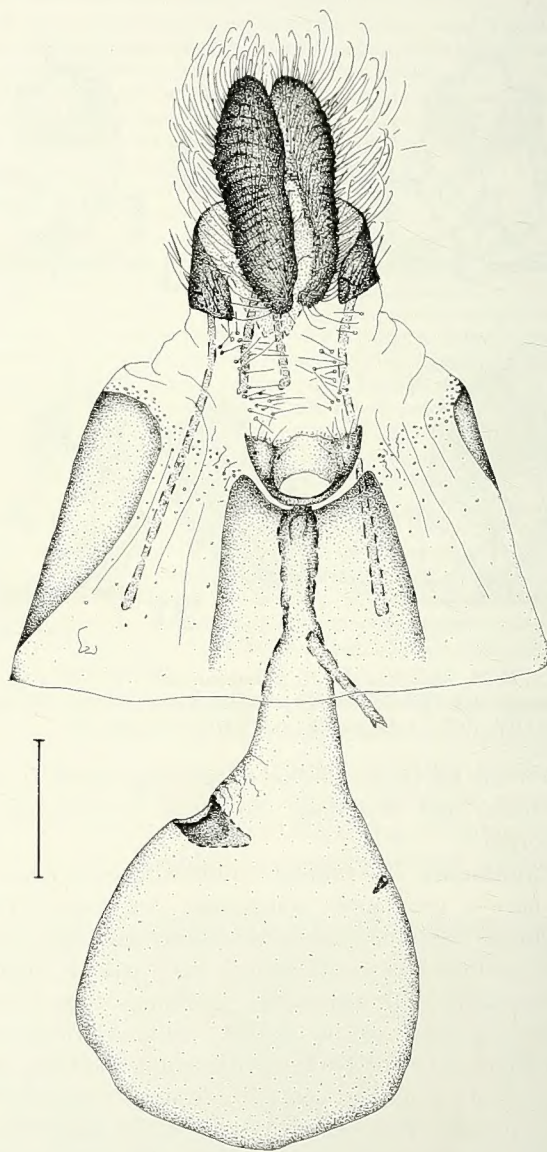
a dark line on the fold or a chevron shaped mark at the end of the cell. Male genitalic characters separating *totana* and *taosana* include: subtle differences in shape of cucullus (Figs. 16, 19), distinctly different shape of uncus, and number of cornuti in vesica (10 for *totana* vs. 5 for *taosana*). *Eucosma totana* is easily separated from *popana* and *powelli* by the presence in the latter two species of a stout spine at the ventral angle of the cucullus. Females of *taosana* are not known, but the sterigmata (Figs. 32, 37, 34) of *totana*, *popana* and

powelli are easily distinguished from one another.

Description. Head: Scales of frons and vertex white, sparsely marked with pale gray; labial palpus porrect, length ca. 3× eye diameter, second segment with medial surface and dorsal margin white, lateral surface pale brownish gray, scales of ventral and dorsal margins long and slender, concealing third segment; antenna white. **Thorax:** Scales of dorsal surface and tegulae white basally and apically, brownish gray medially, producing a speckled effect; ventral surface and hindlegs white, fore and midlegs white posteriorly, brown to pale brown anteriorly, with white annular markings on tarsus and tibia. **Forewing** (Figs. 7, 8): ♂ FWL 8.7-12 mm (mean = 10.1, n = 68), AR = 3.2, CFR = 0.27, ♀ FWL 7.4-10.5 mm (mean = 8.9, n = 18), AR = 3.11; costa nearly straight, apex acute, termen weakly convex; dorsal

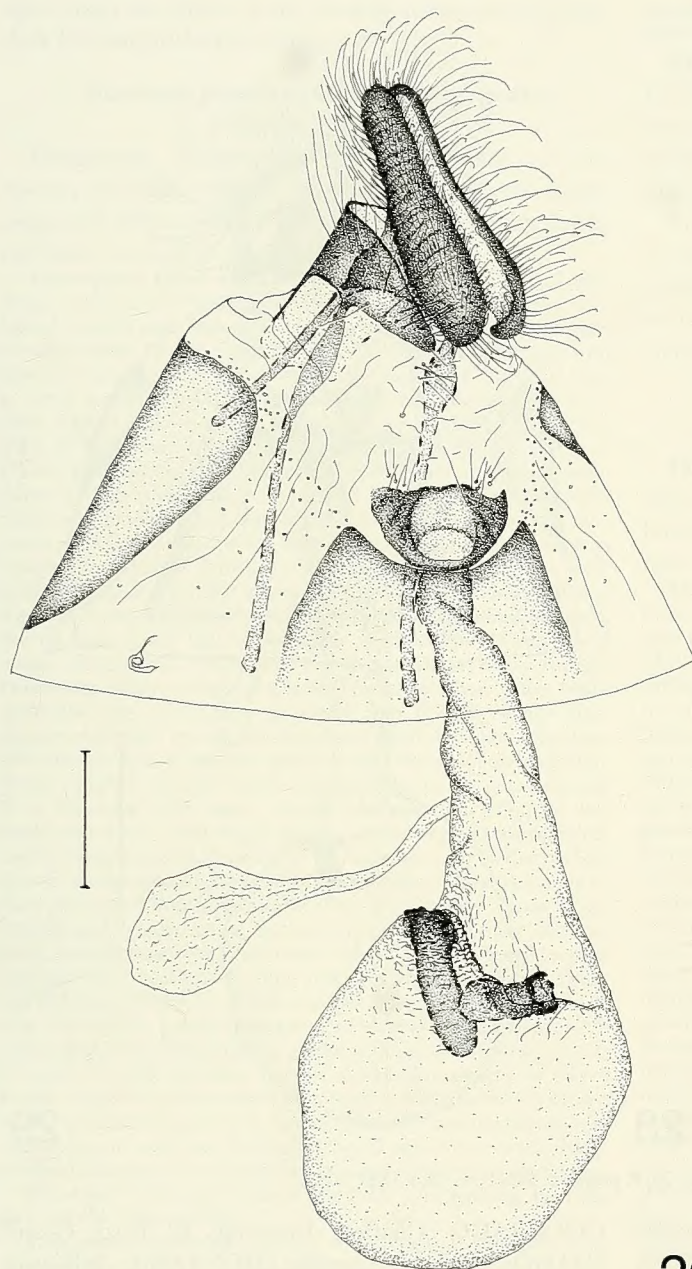


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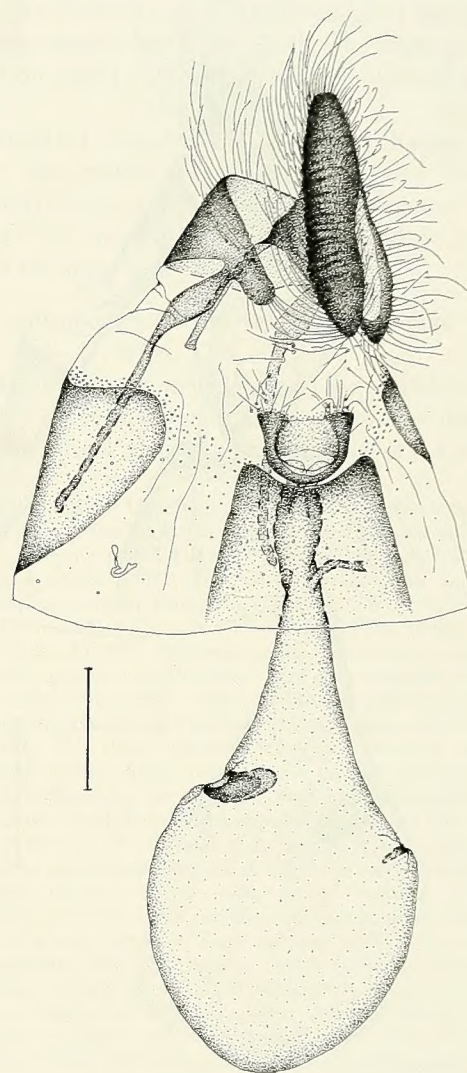


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FIGS. 24-25. Female genitalia. 24, *P. emaciatana*, slide DJW 989. 25, *E. larana*, slide DJW 789.



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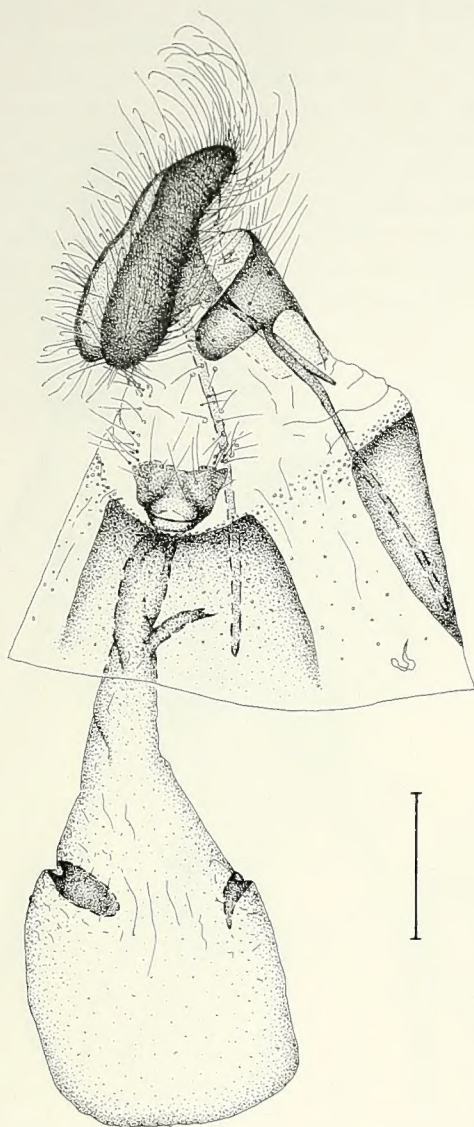


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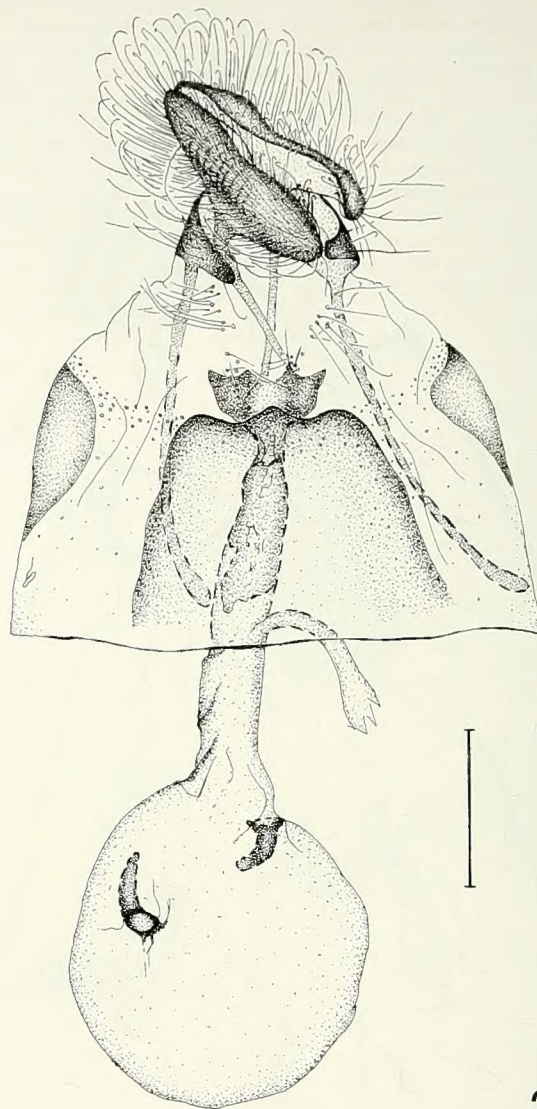
FIGS. 26-27. Female genitalia. 26, *E. piperata*, slide DJW 1061. 27, *E. nordini*, slide DJW 1073

surface white with brown to brownish-black irrorations on basal two-thirds and five brownish-black marks, the first a subbasal mark on fold, sometimes extending weakly to dorsum, often bordered distally by a thin line of black scales, the second a very thin line along fold from subbasal mark to tornus, the third a triangular mark based on fold and projecting anteriorly along basal margin of ocellus, the fourth a longitudinally elongate mark anterior to ocellus, narrowing basally and extending into cell, the fifth a chevron on distal margin of cell, sometimes connecting anteriorly to mid costa and posteriorly to line on fold, often divided medially by aforementioned longitudinal mark; ocellus bordered on basal, distal and tornal margins with lustrous, pale, yellow-brown to yellow-gray bars, white central field crossed by up to four, black, longitudinal dashes; costal margin brownish black,

crossed by numerous paired white strigulae, numbers four through nine usually sharply delineated; dorsal margin with 10-12, small, evenly spaced, brownish-black marks; scales along terminal margin white with subapical black markings, fringe usually whiter with more extensive dark markings between M1 and M3. **Abdomen:** Scales on posterior margin of eighth segment in females brownish black with white apices. **Hindwing:** Uniformly pale brownish gray with lighter fringe. **Male genitalia** (Fig. 16): Uncus triangular, dorsal surface setose, posterior surface developed into medial wedge-shaped ridge, dorsolateral shoulders of tegumen well developed; socii long, flat, and densely setose; aedeagus tapered distally, vesica with ca. 10 deciduous cornuti ($n = 13$); valva with costal margin concave, apex and ventral angle evenly rounded, distal margin convex, invagination of ventral



28



29

FIGS. 28-29. Female genitalia. 28, *E. totana*, slide DJW 1028. 29, *P. popana*, lectotype, slide DJW 1085.

margin moderate, NR = 0.6, cucullus with densely setose medial surface, sacculus and margin of basal opening moderately setose. **Female genitalia** (Fig. 28): Papillae anales facing laterally and densely setose, surfaces finely ridged transversely, setae on medial margins with hooked apices, those on lateral margins twice as long and curving ventrally; posterior margin of tergum VIII with 3-4 rows of setae; lamella antevaginalis (Fig. 32) ringlike and very weakly sclerotized, lamella postvaginalis well developed, width of posterior margin ca. 2× ostium diameter, posterolateral corners acute, a depressed trough from mid posterior margin to ostium; membrane between sterigma and ventral extremities of tergum VIII setose; sternum VII with length of posterior margin ca. 3× ostium diameter, roundly invaginated to depth of one-third length of sterigma, approximate to sterigma medially; ductus bursae constricted anterior to ostium; corpus bursae with two signa.

Distribution and biology. My study sample included 128 specimens (105 ♂, 23 ♀) from the following states and counties: ARIZONA: Coconino;

COLORADO: Chaffee, Fremont, El Paso, Grand; IDAHO: Lincoln, Oneida; MONTANA: Jefferson; NEW MEXICO: Santa Fe; OREGON: Harney; UTAH: Juab, Sanpete; WYOMING: Albany. I have occasionally found this species to be abundant in sagebrush habitat at elevations between 5000' and 8000'. Brown et. al. (1983) reported *Chrysothamnus nauseosus* (Pall.) Britt. (Asteraceae) as a larval host in Idaho.

Comments. The forewing markings are stable, but the overall appearance of *totana* varies from very pale tan to medium brown. In lighter specimens the brown irrorations are restricted to the basal one-third of the wing, the median area is mostly pale yellowish white to white, and the markings are orangish brown. Darker

specimens are much more densely irrorated and have dark brownish-black markings.

***Eucosma piperata* Wright, new species**

(Figs. 4, 18, 26, 35)

Diagnosis. Reasonably fresh specimens of this species are readily identified by forewing pattern: white, peppered with minute black specks, with brown marks on distal one-half of costa.

Description. **Head:** Frons and vertex white, a small patch of pale-brown scales anterior to eye; labial palpus with medial surface white, lateral surface pale brown; antenna white, scape sometimes pale brown dorsally. **Thorax:** Dorsal and ventral surfaces white; legs with anterior surfaces pale brown, posterior surfaces white, and distal ends of tarsal segments lightly ringed with white. **Forewing** (Fig. 4): ♂ FWL 10.8–11.5 mm (mean = 11.2, $n = 6$), AR = 3.11, CFR = 0.32, ♀ FWL 11.5–13.5 mm (mean = 12.6, $n = 8$), AR = 2.99; distal three-fourths of costa straight, apex mildly acute, termen weakly convex; dorsal surface white, sparsely speckled with black scales between radial vein and dorsum, costal strigulae delimited by narrow, brown, costal marks but otherwise not distinguishable from ground color, a conspicuous, oblique, brown mark at apex; ocellus obscure, variably marked on basal and distal margins by a few black and brown scales, respectively, ca. three, black, weakly expressed, longitudinal dashes in central field; costal fold of male pale grayish brown along costal margin; fringe scales white basally, very pale orange brown distally. **Hindwing:** White, a shade grayer than forewing, fringe white. **Male genitalia** (Fig. 18): Uncus a semicircular dorsally setose lobe, supported laterally by well developed and mildly hunched shoulders; socii densely setose, tapered distally, with lateral margins variably serrate; gnathos a narrow band; vesica with ca. 14 deciduous cornuti ($n = 4$); valva with costal margin concave, apex rounded but moderately acute, distal margin convex, ventral angle gently rounded, ventral invagination shallow, NR = 0.7, cucullus with medial surface densely setose, sacculus sparsely setose, a patch of setae on margin of basal opening. **Female genitalia** (Fig. 26): Papillae anales facing laterally and densely setose, medial margins weakly sinuate, surfaces finely ridged transversely, setae toward lateral margins strongly curved ventrally, those near anal opening with hooked apices; posterior one-half of tergum VIII with ca. four rows of setae; lamella antevaginalis (Fig. 35) ringlike; lamella postvaginalis widening posteriorly to ca. 2× ostium diameter, with triangular, mildly setose, posterolateral corners; sternum VII with posterior margin roundly invaginated to three-fourths length of sterigma and approximate to sterigma; ductus bursae weakly constricted anterior to ostium, gradually widening anteriorly; corpus bursae with two similarly shaped signa, membrane finely wrinkled near signa, interior surface of bursa minutely microtrichiate.

Holotype. ♂, Vineyard, Utah, 9 July 1912, Tom Spalding, genitalia slide USNM 70391, USNM.

Paratypes. **ARIZONA:** Lupton, A. K. Wyatt, 3 July 1951 (1 ♂, genitalia slide DJW 1061). **CALIFORNIA:** Inyo Co., 9 mi. W. Lone Pine, P. D. Hurd & J. A. Powell, 19 July 1961 (1 ♀); Westguard Pass, White Mts., P. Opler & J. A. Powell, 19 July 1968 (1 ♀). **COLORADO:** Mesa Co., Colo. N. Monument, Head of Red Canyon, J. Moore, 3 July 2001 (3 ♂, 1 ♀, ♂ genitalia slide DJW 1132, ♀ genitalia slide DJW1133). **IDAHO:** Oneida Co., Curlew NG, 4 mi ENE of Holbrook, 5050', D. J. Wright, 18 July 2001 (1 ♂, genitalia slide DJW 762). **NEVADA:** Nye Co., Currant Cr. Cpgd., J. Scott, 20 July 1968 (1 ♀), P. Opler & J. A. Powell, 20 July 1968 (2 ♀, genitalia slides T. Gilligan 265, DJW 1288); Lincoln Co., Cathedral Gorge St. Pk., J. Doyen, 12/13 July 1971 (1 ♀). **OREGON:** Baker Co., Burnt River Cyn., 3200', 44E 33.08' N, 117E 39.75' W, C. D. Ferris (1 ♀, genitalia slide DJW 1134). **UTAH:** Vineyard, 4 July 1912 (1 ♀); Vineyard, Tom Spalding, 14 July 1912 (1 ♂, genitalia slide DJW 1058); Juab Co., Eureka, Tom Spalding, 20 July 1911 (1 ♂); Sevier Co., Richfield, 15 June 1930 (1 ♂), 15 July 1930 (1 ♂, genitalia slide DJW 1060). Paratype depositories: CDF, CSU, EME, LACM, USNM, DJW.

Etymology. The specific epithet, deriving from the Latin word for

pepper, refers to the minute black speckling on an otherwise white forewing.

Distribution and biology. The 20 specimens (9 ♂, 11 ♀) reported above suggest that the range of this moth may be restricted to the Great Basin. The flight period extends from mid June through July. The larval host is unknown.

Comments. In some specimens the black speckling is barely discernable, but the brown costal marks, particularly the apical one, are usually conspicuous. The wrinkling of the membrane of the corpus bursae in the vicinity of the signa is variable.

***Eucosma nordini* Wright, new species**

(Figs. 5, 21, 27, 31)

Diagnosis. The immaculate pale yellowish-white forewing is diagnostic for this species. Males have a blackish-gray streak along the anterior edge of the costal fold.

Description. **Head:** Upper frons and vertex very pale yellowish white, labial palpus white, lateral surface of second segment with pale gray shading; antenna white. **Thorax:** Dorsal surface pale yellowish white, ventral surface white, legs pale yellowish white, anterior surfaces sometimes darker. **Forewing** (Fig. 5): ♂ FWL 10–13.7 mm (mean = 11.9, $n = 14$), AR = 3.35, CFR = 0.29, ♀ FWL 10.8–13 mm (mean = 11.5, $n = 5$), AR = 3.13; costa straight, apex acute, terminal margin weakly convex; dorsal surface very pale yellowish white, without markings, fringe white, males with blackish-gray streak along costal edge of fold. **Hindwing:** Pale brownish gray, fringe white. **Male genitalia** (Fig. 21): Uncus semitriangular, apex rounded, lateral margins weakly convex, dorsal surface setose, shoulders of tegumen well developed; socii long, flat, tapering distally, and densely setose; gnathos a narrow band; aedeagus tapering distally, vesica with 4–10 deciduous cornuti ($n = 5$); valva with costal margin concave except for slight, elongate, convex protrusion on cucullus, apex semirectangular, distal margin convex, ventral angle gently rounded, ventral invagination shallow, NR = 0.75, cucullus with medial surface densely setose, sacculus and margin of basal opening moderately setose. **Female genitalia** (Fig. 27): Papillae anales facing laterally and densely setose, surfaces finely ridged transversely, medial margins mildly sinuate, long setae on lateral margins curving ventrally, setae near anal opening shorter with hooked apices; three to four rows of setae on posterior one-third of tergum VIII; lamella antevaginalis (Fig. 31) ringlike; lamella postvaginalis with triangular, setose, posterolateral, corners, posterior margin weakly invaginated medially; sternum VII with posterior margin slightly wider than sterigma, roundly invaginated to one-third length of sterigma and approximate thereto; ductus bursae strongly constricted anterior to ostium, gradually widening toward corpus bursae, corpus bursae with large signum near juncture with ductus bursae and smaller spike-like signum on opposite wall posterior to mid bursa, inner surface minutely microtrichiate.

Holotype. ♂, Wyoming, Albany Co., Medicine Bow NF, 11.5 mi SE Laramie, Jctn. Forest Rds 707 and 705, 4 August 2001, D. J. Wright, 8220', genitalia slide DJW 760, deposited in USNM. Type locality at 41° 11.75' N, 105° 23.7' W.

Paratypes. **COLORADO:** Chaffee Co., Salida, G. M. and J. L. Sperry, 24 August 1938 (1 ♀, genitalia slide DJW1165). **WYOMING:** Albany Co., T15N S73W Sec. 1, 7450', C. D. Ferris, 25 July 2000 (1 ♂), 28 July 2000 (1 ♂, genitalia slide USNM 91928), 30 July 2003 (1 ♂), 5 August 2003 (2 ♂), 9 August 2002 (1 ♂), 9 August 2003 (1 ♂), 10 August 2002 (3 ♂, genitalia slide DJW1077), 10 August 2003 (1 ♂), 11 August 2003 (1 ♂), 13 August 2002 (1 ♂), 14 August 2002 (1 ♂), 15 August 2002 (3 ♂), 15 August 2003 (2 ♂), 16 August 2002 (5 ♂), 17 August 2002 (1 ♂, 1 ♀), 18 August 2002 (1 ♂), 18 August 2003 (2 ♂), 19

August 2002 (5 ♂, 1 ♀), 19 August 2003 (1 ♂, genitalia slide DJW 1078), 22 August 1999 (1 ♀), 22 August 2002 (1 ♂, genitalia slide DJW 1073), 24 August 2002 (1 ♂), 25 August 2002 (1 ♀, genitalia slide DJW 1074); Albany Co., T15N S73W Sec. 1, 2217 Sky View Ln., 7468', J. S. Nordin, 27 July 1994 (1 ♀, genitalia slide DJW 312), 11 August 1995 (1 ♂, genitalia slide DJW 271), 14 August 2001 (1 ♂), 16 August 1999 (1 ♂), 17 August 2002 (1 ♂), 19 August 1995 (1 ♂), 20 August 1998 (1 ♂), 21 August 1998 (1 ♂, genitalia slide J. W. Brown 1173), 28 August 1998 (1 ♂); Albany Co., T15N S71W Sec. 14, E. of Pilot Hill Road, 8600', J. S. Nordin, 25 August 1998 (2 ♂); Albany Co., Upper Blair PG, N. of Rd. 705, J. S. Nordin, 8200', 12 August 2003 (1 ♀); Albany Co., NE of Pole Mtn., S. of Happy Jack Rd., 8320', J. S. Nordin, 12 August 2001 (1 ♂); Albany Co., 1.5 mi NW Woods Landing, Fox Creek, J. S. Nordin, 7600', 31 July 2002 (1 ♂); Albany Co., 8 mi. NE Laramie, Rogers Canyon, M. Pogue, 22 August 1980 (3 ♀, genitalia slide DJW 1135); Albany Co., Medicine Bow NF, 10.5 mi SE Laramie, 8300', D. J. Wright, 4 August 2001 (2 ♂); Albany Co., Medicine Bow NF, 11.5 mi SE Laramie, 8220', D. J. Wright, 4 August 2001 (1 ♂); Teton Co., Grand Teton NP, Teton Sciences School, P. A. Opler, 3 August 2001 (1 ♂); Washakie Co., Tensleep Preserve, T47N R86W S32, 6400', 8 August 1999, C. D. Ferris (3 ♂). Paratype depositories: AMNH, BMNH, CNC, CDF, CSU, EME, JSN, LACM, USNM, DJW, UWY.

Etymology. It is a pleasure to name this species after John S. Nordin, whose extensive collecting around Laramie, Wyoming, has made a significant contribution to our knowledge of the lepidopteran fauna of that region.

Distribution and biology. I examined 115 specimens (104 ♂, 11 ♀) from the following states and counties: COLORADO: Chaffee; WYOMING: Albany, Teton, Washakie. Capture sites range in elevation from 6400' to 8300'. Flight occurs from late July to the end of August. The larval host is unknown.

Eucosma taosana Wright, new species

(Figs. 9, 19)

Diagnosis. The forewing of *taosana* has a conspicuous band of orange-brown scales along the costa and a line of similarly colored scales along 1A+2A. The male genitalia of *taosana* is similar to that of *totana* (Figs. 16, 19), but the apex of the cucullus is more angular and the uncus lacks a wedge shaped posterior projection.

Description. **Head:** Lower frons white, scales of vertex brownish gray medially, lighter toward base and apex; labial palpus with medial surface white, lateral surface brown; antenna brown. **Thorax:** Dorsal surface brown, scales on apex of tegulae brownish black with white apices, ventral surface pale tan, legs with anterior surfaces dark gray-brown, posterior surfaces pale tan, distal extremities of tarsal segments orange with pale tan. **Forewing** (Fig. 9): ♂ FWL 7.5-9.5 mm (mean = 8.0, n = 12), AR = 3.19, CFR = 0.31; costa and termen nearly straight, apex acute; dorsal surface brown with brownish-black markings, a band of orange-brown coloration from base to apex between costa and radial vein, a narrow similarly colored band from base to tornus along 1A+2A, a brownish-black, outwardly oblique, subbasal mark on dorsum extending forward into cell, a triangular, brownish-black, subternal mark on dorsum projecting anteriorly along basal margin of ocellus, both marks divided by orange-brown line along 1A+2A, a narrow elongate patch of white-tipped, dark grayish-brown scales anterior to ocellus, extending and tapering basally to middle of cell, mildly constricted at distal end of cell; ocellus with basal, distal and tornal margins pale yellowish brown to yellowish gray, central field white to pale brown, crossed longitudinally by 3-4 brownish-black dashes, the latter often connected in zig-zag pattern; distal one-half of costa usually with four, sharply defined, paired, white strigulae, costal fold on male brownish black; termen with band of white-tipped

brownish-black scales from apex to tornus, fringe scales similarly marked near apex, lighter and more uniformly brownish gray toward tornus. **Male genitalia** (Fig. 19): Uncus triangular and dorsally setose, divided medially by shallow indentation; dorsolateral shoulders of tegumen well developed and hunched; aedeagus long, slender, and tapering distally, vesica with 4-5 deciduous cornuti (n = 9); gnathos a narrow band; valva with costal margin concave, apex rounded but moderately acute, distal margin convex, with ca. 8 stout setae along ventral two-thirds, ventral angle rounded, ventral invagination moderate, NR = 0.61, cucullus with distal one-half of medial surface densely setose, saccus moderately setose, margin of basal opening with setose medial projection.

Holotype. ♂, New Mexico, Taos Co., S. Side US 64, 10 mi. SE Tres Piedras, 7550', 11 August 1999, D. J. Wright, genitalia slide DJW 1035, deposited in USNM. Type locality at 36° 34.5' N, 105° 48.2' W.

Paratypes. **NEW MEXICO:** Same data as holotype (17 ♂, genitalia slides DJW 528, 1034); Luma Co., Deming, 16-23 August (2 ♂, genitalia slides USNM 70399, DJW 1070); Fort Wingate, 24-30 June (1 ♂, genitalia slide USNM 70396), 24-31 July (3 ♂, genitalia slide USNM 70398). **UTAH:** Tooele Co., Stockton, Tom Spalding, 30 August 1904 (1 ♂, genitalia slide DJW 1064). Paratype depositories: AMNH, BMNH, CNC, CSU, EME, LACM, USNM, DJW.

Etymology. The specific epithet refers to Taos County, New Mexico.

Distribution and biology. Of the 29 specimens examined, one is from central Utah and the rest are from New Mexico. Capture dates range from late June through August. The type locality is open sagebrush habitat at an altitude of 7550 feet. The larval host is unknown.

Pelochrista emaciatana (Walsingham), new combination

(Figs. 1, 10, 13, 17, 24, 33)

Paedisca emaciatana Walsingham 1884:137, pl. IV, Fig. 7.

Eucosma emaciatana: Fernald [1903]:460; Barnes and McDunnough 1917:171; McDunnough 1939:46; Powell 1983:34.

Eucosma perpropinqua: Heinrich 1929:8; McDunnough 1939:47, **new synonymy**.

Pelochrista perpropinqua: Powell 1983:35.

Types. *Paedisca emaciatana*. Lectotype here designated (Figs. 1, 13): ♂, Arizona, Morrison, 1882, genitalia slide 11571, BMNH. Paralectotypes: same data as lectotype, (2 ♂, BMNH). *Eucosma perpropinqua*. Holotype: ♂, Arizona, Pima Co., Indian Oasis, Sells Post Office, 15-30 April 1923, O. C. Poling, genitalia slide 72797, USNM. Paratypes: same site and collector as holotype, 1-15 April 1923 (3 ♀, genitalia slides DJW 809, 955, USNM; 1 ♀, CNC), 15-30 April 1923 (1 ♀, USNM; 1 ♀, AMNH).

Diagnosis. Reasonably fresh specimens can be identified on the basis of forewing pattern (Fig. 10), but dissection is recommended for positive determination. Males are distinguished by the general shape of the valva and the size and position of the ventral spike (Fig. 17), females by the sclerotized plate on the dorsolateral surface of the corpus bursae, the presence of only one

signum, and the shape of the sterigma (Figs. 24, 33).

Description. Head: Frons and vertex white, scales anterior to eye light brown; labial palpus elongate, lateral profile triangular, length more than 2× eye diameter, first segment and medial surface of second segment white, scales on lateral surface and dorsal margin of second segment pale brown with white apices, scales of second segment concealing third segment; antenna white. **Thorax:** Dorsal surface white with pale-brown shading, scales of tegulae light brown with white apices, ventral surface white, legs light brown with white tarsal annulations. **Forewing** (Figs. 1, 10): ♂ FWL 10.8-13 mm (mean = 11.5, n = 7), AR = 3.1, CFR = 0.27, ♀ FWL 7.9-9.9 mm (mean = 9.4, n = 6), AR = 3.3; costa straight, vertex acute; dorsal surface white with brown markings, appearing streaked longitudinally, a dark-brown, outwardly oblique, subbasal mark on fold, a brown pretornal mark on dorsum, often one or more variably expressed, disjunct, brown marks between mid costa and pretornal mark, and an elongate patch of pale brown scales with white apices anterior to ocellus and connected by oblique spur of similar scaling to brown apical mark; ocellus obscure, white to pale brown, crossed longitudinally by three light-brown streaks, the latter often marked medially by a few brownish-black scales; termen with several rows of pale brown scales with white apices, the latter preceded basally by a streak of white scales from distal margin of ocellus to apex; distal one-half of costa with four indistinct, white, paired strigulae, merging into light post-costal streak from mid costa to apical mark; male costal fold darker than adjacent forewing scaling. **Hindwing:** Uniformly brownish gray with pale white fringe. **Male genitalia** (Figs. 13, 17): Uncus a dorsally setose convex lobe, shoulders of tegumen moderately tapered; socii curving dorsally and moderately setose; aedeagus developed distally, vesica with no indication of cornuti (n = 10); valva with costal margin concave, apex evenly rounded, outer margin convex, ventral angle with well developed projection supporting a stout spine, usually a spine of similar size and several smaller spines on distal margin of cucullus, ventral invagination moderate, NR = 0.7, cucullus with distal two-thirds of medial surface densely setose, sacculus moderately setose. **Female genitalia** (Fig. 24): Papillae anales facing laterally and densely setose, medial margins mildly sinuate, surfaces finely ridged transversely, long setae on lateral margins strongly curved ventrally; lamella antevaginalis (Fig. 33) ringlike and very weakly sclerotized; lamella postvaginalis well developed, depressed medially, with variably invaginated posterior margin and sharply acute anterolateral projections; sternum VII with posterior margin weakly invaginated and closely approximate to sterigma; ductus bursae uniformly narrow, constricted anterior to ostium; corpus bursae with large sclerotized patch on dorsolateral surface at juncture with ductus bursae, a large signum on ventral surface, and a faint indication of a reduced signum at center of anterior margin of sclerotized patch.

Distribution and biology. I examined 96 specimens (66 ♂, 30 ♀): one each from San Bernadino Co., California, Clark Co., Nevada, and Kimble Co., Texas; the rest (to the extent determinable by specimen data) from Cochise, Pima, Pinal, and Santa Cruz Counties in Arizona. Three specimens had capture dates in September or October; the others were collected between early March and mid June. Ninety percent of the records were dated between 1 April and 31 May. No larval host information has been reported.

Pelochrista popana (Kearfott)

(Figs. 11, 20, 29, 37)

Eucosma popana Kearfott 1907:31; Barnes & McDunnough 1917:169; Heinrich 1923:109; McDunnough 1939:47.

Eucosma carcharias: Meyrick 1912:35.

Pelochrista popana: Powell 1983:35.

Types. Lectotype designated by Klots (1942): ♀, Stockton, Utah, Tom Spalding, 3 July 1904, genitalia slide DJW 1085, AMNH. Paralectotypes: UTAH: Stockton, Tom Spalding, 1 June 1904 (3 ♂, AMNH; 1 ♀, USNM), 8 June 1904 (2 ♂, USNM), 10 June 1904 (2 ♂, USNM), 14 June 1904 (2 ♂, AMNH; 1 ♂, USNM), 15 June 1904 (1 ♂, USNM), 28 June 1904 (1 ♀, AMNH), 3 July 1904 (2 ♀, AMNH).

Diagnosis. The forewing maculation of *popana* is grayish-black, as opposed to brown in *totana*, *taosana*, and *powelli*. The dark mark anterior to the ocellus nearly always connects to an apical dash of the same color, often connects to costa, and frequently extends along distal edge of ocellus toward tornus, forming a distinctive Y-shaped mark. The shapes of the valva (Fig. 20) and sterigma (Fig. 37) separate *popana* from the other species considered here.

Description. Head: Lower frons white, scales of upper frons and vertex long, gray to brownish gray medially, with lighter apices; labial palpus with basal segment and medial surface of second segment white, lateral surface of second segment gray to brownish gray, third segment concealed by scales of second segment; antenna grayish white, often darker distally. **Thorax:** Dorsal surface and tegulae with brownish-gray, white-tipped scales, ventral surface white, legs with anterior surfaces brownish gray, posterior surfaces white, tarsal segments with white distal annulations. **Forewing** (Fig. 11): ♂ FWL 8-9.8 mm (mean = 8.6, n = 12), AR = 3.21, CFR = 0.31, ♀ FWL 6.7-8.3 mm (mean = 7.4, n = 19), AR = 3.21; costa weakly convex, apex acute, termen weakly convex; dorsal surface white with brownish-black to brownish-gray markings, basal and median areas white and variably irrorated with brownish gray, an outwardly oblique subbasal mark extending from dorsum to cell, a broken median fascia consisting of three marks, the first at mid costa, the second at distal end of cell, the third semitriangular and projecting anteriorly from pretornal portion of dorsum along basal margin of ocellus, the first two median marks often connected, the latter two usually separated by narrow band of white scales, an elongate patch of white-tipped, black to brownish-gray scales anterior to ocellus, usually connected to apex by oblique dash of similar coloration; ocellus with basal, distal and tornal margins pale pinkish brown, central field a narrow, vertical, light brown streak, crossed longitudinally by ca. 4 black dashes; distal one half of costa with four paired white strigulae, costal fold of male dark gray, fringe scales white basally and apically, black to brownish-gray medially. **Abdomen:** Females with dark gray scales on posterior margin of eighth segment. **Hindwing:** Uniformly brownish gray, fringe lighter. **Male genitalia** (Fig. 20): Uncus dorsally setose and semitriangular, apex sometimes weakly indented; socii long and setose, curving dorsally; aedeagus long, tapering distally, vesica with 3-6 deciduous cornuti (n = 4); valva with costal margin concave, apex nearly right angled but rounded, distal margin convex with 2-3 stout spines, ventral angle developed into triangular lobe supporting 1 or 2 stout spines, ventral invagination broad and shallow, NR = 0.7, cucullus with medial surface moderately setose, sacculus sparsely setose, margin of basal opening with weakly developed setose projection. **Female genitalia** (Fig. 29): Papillae anales facing ventrolaterally and densely setose, surfaces finely ridged transversely, medial margins sinuate, setae on lateral margins long, curving ventrally, those near anal opening shorter, with hooked apices; sterigma (Fig. 37) with anterior margin very weakly sclerotized, lamella postvaginalis extending laterally to width of ca. 3× ostium diameter, widening posteriorly, length ca. 0.5× width, posterior margin with scalloped appearance due to sharply acute posterolateral corners and concave medial invagination, a very shallow trough from mid

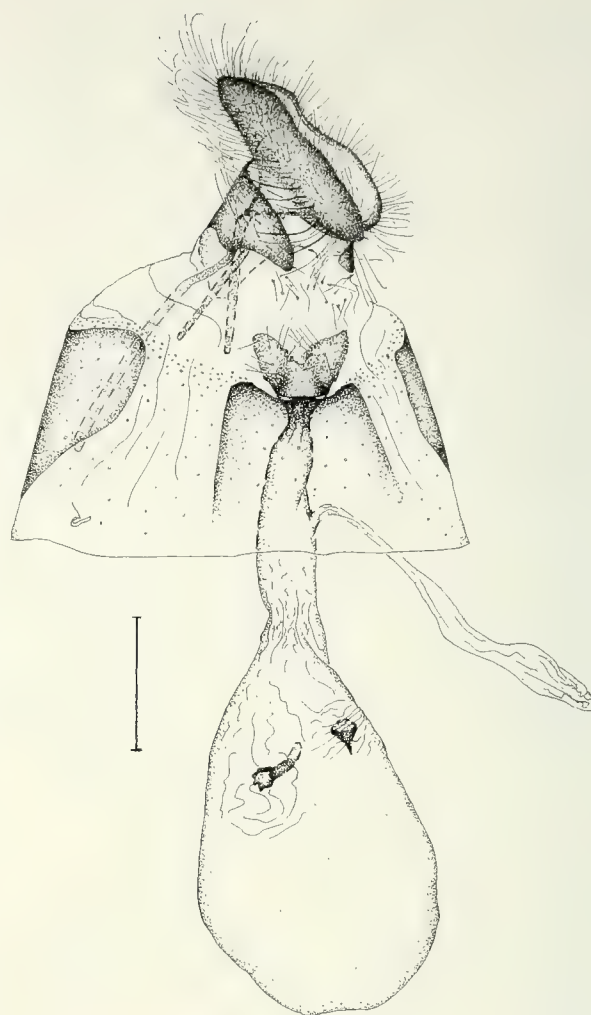
posterior margin to ostium, surface finely microtrichiate; sternum VII with posterior and lateral margins strongly sclerotized, posterior margin with medial triangular projection overlapping ostium; ductus bursae of nearly uniform width, sclerotized from constriction anterior to ostium to ductus seminalis; corpus bursae with two similarly sized signa, membrane variably crinkled around signa, interior surface minutely microtrichiate.

Distribution and biology. I examined 167 specimens (146 ♂, 21 ♀) from the following states and counties: COLORADO: Chaffee, Grand, Larimer, Mesa; IDAHO: Blaine; MONTANA; NEVADA: Lander, White Pine; NEW MEXICO: Taos; UTAH: Cache, Garfield, San Juan, Tooele, Uintah; WYOMING: Albany, Carbon, Fremont, Park, Sublette, Teton. They document a flight period from early June to late August. No larval host has been reported.

Pelochrista powelli Wright, new species
(Figs. 12, 22, 23, 30, 34)

Diagnosis. This moth has a pale brown appearance. By contrast, *popana* is brownish-black to gray, with considerable contrast between markings and ground color. The forewing pattern of *powelli* lacks the chevron shaped mark at the end of the cell in *totana* and the orange-brown scaling along the costa and along 1A+2A in *taosana*. In females of *powelli*, the scales on the posterior margin of the eighth abdominal segment are brown and inconspicuous, they are brownish-black to gray in *popana*. The v-shaped posterior margin of the sterigma separates *powelli* from the other species considered here.

Description. **Head:** Lower frons pale tan, scales of vertex white distally, shading to tan basally; labial palpus tan to pale brown; antenna pale tan. **Thorax:** Dorsal surface pale brown, ventral surface pale tan, legs with anterior surfaces pale brown, posterior surfaces white to tan, distal ends of tarsal segments ringed with pale tan. **Forewing** (Fig. 12): ♂ FWL 7.1–10.5 mm (mean = 8.7, n = 10), AR = 3.3, CFR = 0.26, ♀ FWL 8.2–9.2 mm (mean = 8.8, n = 5), AR = 3.11; costa weakly convex, apex acute, termen straight to weakly convex; dorsal surface pale tan with brown markings, a brownish-black subbasal mark on fold, a thin brown line along fold from subbasal mark to tornus, a narrow, triangulate, brown mark based on fold and projecting toward apex along basal margin of ocellus, an elongate patch of white-tipped brownish-black scales anterior to ocellus, extending basally through distal one-half of cell, usually constricted and darker at distal end of cell; ocellus obscure, variably bordered on basal, distal and tornal margins with pale pinkish-tan bars, central field white, crossed by 4–6 brownish-black dashes that are often joined in zig-zag pattern; distal two-thirds of costa with numerous white strigulae, delineated by brown costal marks and thin brown striae, male costal fold brownish black; termen with band of white-tipped brownish-black scales extending from apex to tornus, fringe scales lighter with pale-brown medial markings. **Hindwing:** Pale gray-brown with paler fringe. **Male genitalia** (Figs. 22, 23): Uncus semitriangular with rounded apex, dorsal surface setose; tegumen long, dorsolateral shoulders well developed and hunched; socii long, flat, tapering distally, and moderately setose; gnathos a narrow band; aedeagus long, tapered distally, vesica with 4–9 deciduous cornuti (n = 7); valva with costal margin weakly concave, apex rounded to angular, distal margin convex, ventral angle with triangular projection supporting stout spine, neck long and narrow, NR = 0.5, ventral invagination broad and moderate, cucullus with densely setose medial surface and 3–5 stout spines on distal margin, saccus moderately setose, margin of basal



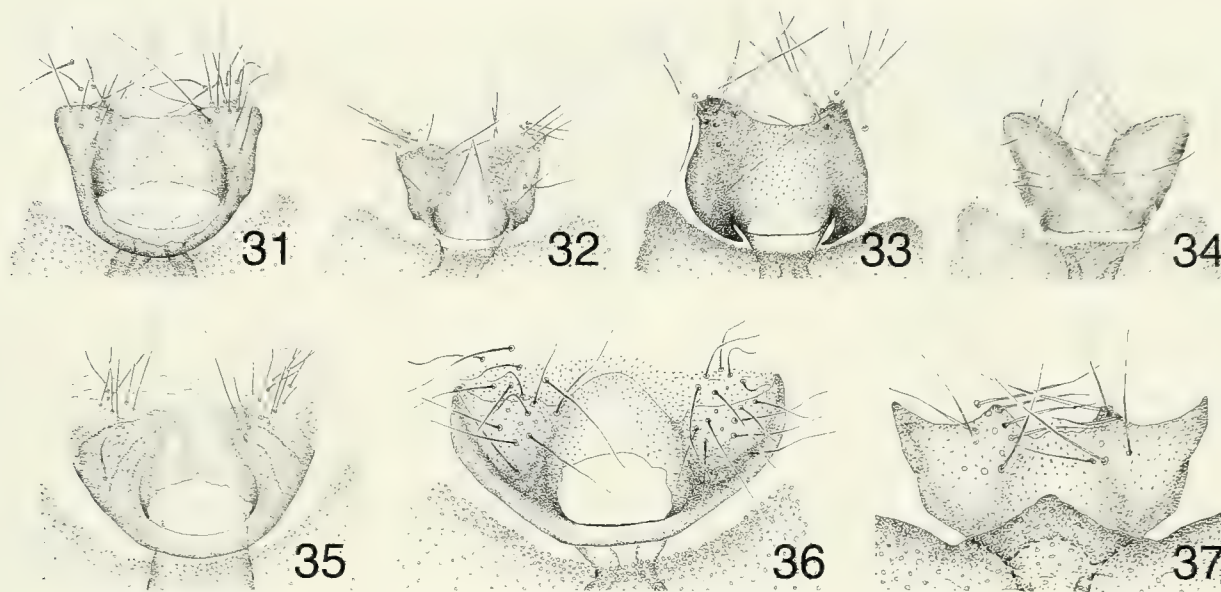
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FIG. 30. Female genitalia. 30, *P. powelli*, slide DJW 1024.

opening with weakly developed setose projection. **Female genitalia** (Fig. 30): Papillae anales facing posterolaterally and densely setose, medial margins sinuate, surfaces very finely ridged transversely, setae on lateral margins long and curving ventrally, those near anal opening shorter with hooked apices; posterior one-half of tergum VIII with 4–5 rows of setae; sterigma (Fig. 34) with anterior margin very weakly sclerotized, lamella postvaginalis developed posterolaterally into triangular projections, posterior margin with v-shaped medial invagination, surface finely microtrichiate; sternum VII with posterior margin concavely invaginated except for mild, convex, medial, projection overlapping ostium; ductus bursae narrow, constricted anterior to ostium; corpus bursae with two signa, inner surface minutely microtrichiate.

Holotype. ♂, Idaho, Oneida Co., Curlew NG, 4 mi. ENE of Holbrook, Jctn. Forest Rds. 056 and 057, 5050', 7 July 2001, D. J. Wright, genitalia slide DJW 1032, deposited in USNM. Type locality at 42° 11.35' N, 112° 34.92' W.

Paratypes. IDAHO: Oneida Co., Curlew NG, 4 mi. ENE of Holbrook, 5050', D. J. Wright, 25 July 2003 (2 ♂, genitalia slide DJW1027), 26 July 2003 (2 ♂, 1 ♀); Oneida Co., Curlew NG, T14S R32E S30, D. J. Wright, 28 July 2003 (4 ♀, genitalia slides DJW1024, 1029). UTAH: Daggett Co., 4 mi. S. of Manila, G. J. Balogh, 20 July



FIGS. 31-37. Sterigmata of specimens illustrated in Figs. 24-30. 31, *E. nordini*. 32, *E. totana*. 33, *P. emaciatana*. 34, *P. powelli*. 35, *E. piperata*. 36, *E. larana*. 37, *P. popana*.

1994 (5 ♂, genitalia slides DJW 697, 705, 707); Juab Co., Eureka, Tom Spalding, 18 August 1911 (1 ♂, genitalia slide DJW1069); Garfield Co., 3 mi. W. Bryce Jct., 2300m, J. A. Powell, 28/29 June 1992 (1 ♂, genitalia slide EME 5755); Garfield Co., Kings Cr. campgr., 15 km SW Bryce Jct., 2300m, J. A. Powell, 18 July 1993 (12 ♂, genitalia slide EME 5756). Paratype depositories: BMNH, CNC, EME, GJB, USNM, DJW.

Etymology. This species is named after J. A. Powell, who collected nearly half of the specimens in the type series.

Distribution and biology. The 29 specimens (24 ♂, 5 ♀) reported above were collected in southeastern Idaho and Utah, suggesting a Great Basin distribution for this insect. The type locality is open sage brush habitat. The larval host is unknown.

Comments. The shape of the male valva is variable (Figs. 22, 23), the cucullus illustrated in Fig. 22 being the most angular of the nine I examined. Forewing color also varies from very light tan in the specimens from Idaho to a pale brown in those from Utah.

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LITERATURE CITED

- BAIXERAS, J. 2002. An overview of genus-level taxonomic problems surrounding *Argyroproctae* Hübner (Lepidoptera: Tortricidae), with description of a new species. *Ann. Entomol. Soc. Am.* 95(4):422-431.
- BARNES, W & J. McDUNNOUGH. 1917. Checklist of the Lepidoptera of Boreal America. Herald Press, Decatur, Illinois. 392 pp.
- BROWN, R. L., J. F. G. CLARKE, & D. H. HABECK. 1983. New host records for Olethreutinae (Tortricidae). *J. Lepid. Soc.* 37:224-227.
- BROWN, R. L. & J. A. POWELL. 1991. Description of a new species of *Epiblema* (Lepidoptera: Tortricidae: Olethreutinae) from coastal redwood forests in California with an analysis of the forewing pattern. *Pan-Pacific Entomol.* 67:107-114.
- FERNALD, C. H. [1903]. In Dyar, H. G., A list of North American Lepidoptera. U.S. Nat. Mus. Bull. 52:1-723.
- HEINRICH, C. 1923. Revision of the North American moths of the subfamily Eucosminae of the family Olethreutidae. U.S. Nat. Mus. Bull. 123:1-298.
- . 1929. Notes on some North American moths of the subfamily Eucosminae. U.S. Nat. Mus. Proc. 75:1-23.
- KEARFOTT, W. D. 1907. New North American Tortricidae. *Trans. Amer. Entomol. Soc.* 33:1-98.
- KLOTS, A. B. 1942. Type material of North American microlepidoptera other than Aegeriidae in The American Museum of Natural History. *Bull. Amer. Mus. of Nat. Hist.* 79:391-424.
- MCDUNNOUGH, J. 1939. Check List of the Lepidoptera of Canada and the United States of America. Part II. Microlepidoptera. *Mem. South. Calif. Acad. Sci.* 2:3-171.
- MEYRICK, E. 1912. On some impossible specific names in microlepidoptera. *Entomol. Monthly Mag., Ser. 2*, 48:32-36.
- POWELL, J. A. 1983. Tortricidae, pp. 31-41. In Hodges, R. W. et al. (eds.), *Check list of the Lepidoptera of America north of Mexico*. E. W. Classey & Wedge Entomol. Res. Foundation. London, England.
- WALSINGHAM, LORD. 1879. Illustrations of typical specimens of Lepidoptera Heterocera in the collection of the British Museum. Part IV. North American Tortricidae. 84 pp. + 17 pls. Dept. Zoology, British Museum, London.
- . 1884. North American Tortricidae. *Trans. Entomol. Soc. Lond.* 1884:121-147 + 1 pl.

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REDISCOVERY OF *ACTINOTE ZIKANI* (D'ALMEIDA) (NYMPHALIDAE, HELICONIINAE, ACRAEINI): NATURAL HISTORY, POPULATION BIOLOGY AND CONSERVATION OF AN ENDANGERED BUTTERFLY IN SE BRAZIL

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ABSTRACT. *Actinote zikani* (D'Almeida) (Nymphalidae, Heliconiinae, Acraeini) was rediscovered in 1991 in Paranapiacaba, São Paulo, 40 years after its original description (based on specimens from the Boracéia Ecological Station, Salesópolis, São Paulo); 49 years after its last collection, and studied during three years. The adults go through two yearly generations, one in March (earlier than the other species of *Actinote* in the region) and the other in November (bivoltinism). The mean residence of the adults is less than one week, and the sex ratio in the field is male biased. The only known host plant for the species is *Mikania obsoleta* (Asteraceae), and the immature stages are similar to those known for other species of *Actinote*. The range of *A. zikani* is within one of the most densely human populated regions in Brazil, making urgent the creation of effective preserved areas where colonies of this species are known.

Additional key words: Atlantic forest, Bivoltinism, *Mikania*, Neotropical

In 1941 and 1942, Romualdo Ferreira D'Almeida collected 10 individuals of a dark *Actinote* Hübner at the Estação Biológica de Boracéia in Salesópolis, São Paulo, which were misidentified as *Actinote morio* (D'Almeida, 1943). Later, notified by J. F. Zikán (a field naturalist who lived near Itatiaia, RJ) D'Almeida corrected himself, recognizing the status of this species and describing it as *Actinote zikani* (D'Almeida, 1951). This species was described based on material collected by D'Almeida from Boracéia (Salesópolis) and one male collected by Roberto Spitz from Alto da Serra de Santos, SP in 1941. A survey revealed that the 11 specimens cited by D'Almeida are now in the Museu de Zoologia da Universidade de São Paulo (MZUSP; Lamas 1973) and the Museu de Zoologia da Universidade Federal do Paraná (Mielke & Casagrande 1986). Additionally, KB saw another 18 specimens collected by R. Spitz from the Alto da Serra de Santos, in the collection of the Natural History Museum (London). From 1985 to 1990, *A. zikani* was searched for intensively by RBF and AVL in the type-locality in April-May and November-December, and also in other sites with the same environmental characteristics (Francini 1992), but none were seen. The only new information was from KB who saw a possible male of

this species on the wing in April 1981 on the edge of the road from Tapiraí to Sorocaba, in southern São Paulo state, about 1000 m altitude in a very wet forest. Because of the difficulty in finding extant colonies of this species, KB proposed the inclusion of *A. zikani* on the list of Brazilian species possibly threatened with extinction (Bernardes et al. 1990; Brown 1991), and since then, *A. zikani* has been classified as critically endangered (SP-SMA 1998, MMA 2003). With intensive searching, finally on 16 March 1991 (1100 h), on a routine trip, RBF and AVL found a male flying at the summit of the Serra do Mar, 20 km northeast of the city of Santos, São Paulo. With data from this locality, the present paper describes the natural history and population biology of *A. zikani*, information important to the conservation of the species and its habitat.

STUDY SITE AND METHODS

The population studied was located in the Santo André municipality, São Paulo State, near the village of Paranapiacaba. Most field work was carried out in a place east of Paranapiacaba, along a road 2500m long (SW-NE following the orientation of the mountain chain), paved with concrete blocks, connecting two groups of towers (television and microwaves) on peaks of Serra do Mar reaching 1200 m (Fig. 1). Because of the high rainfall, the road on the summit was built with a good drainage network; there are also four small creeks running across the road. Sometimes the road and drains were cleared, but the trees next to them were

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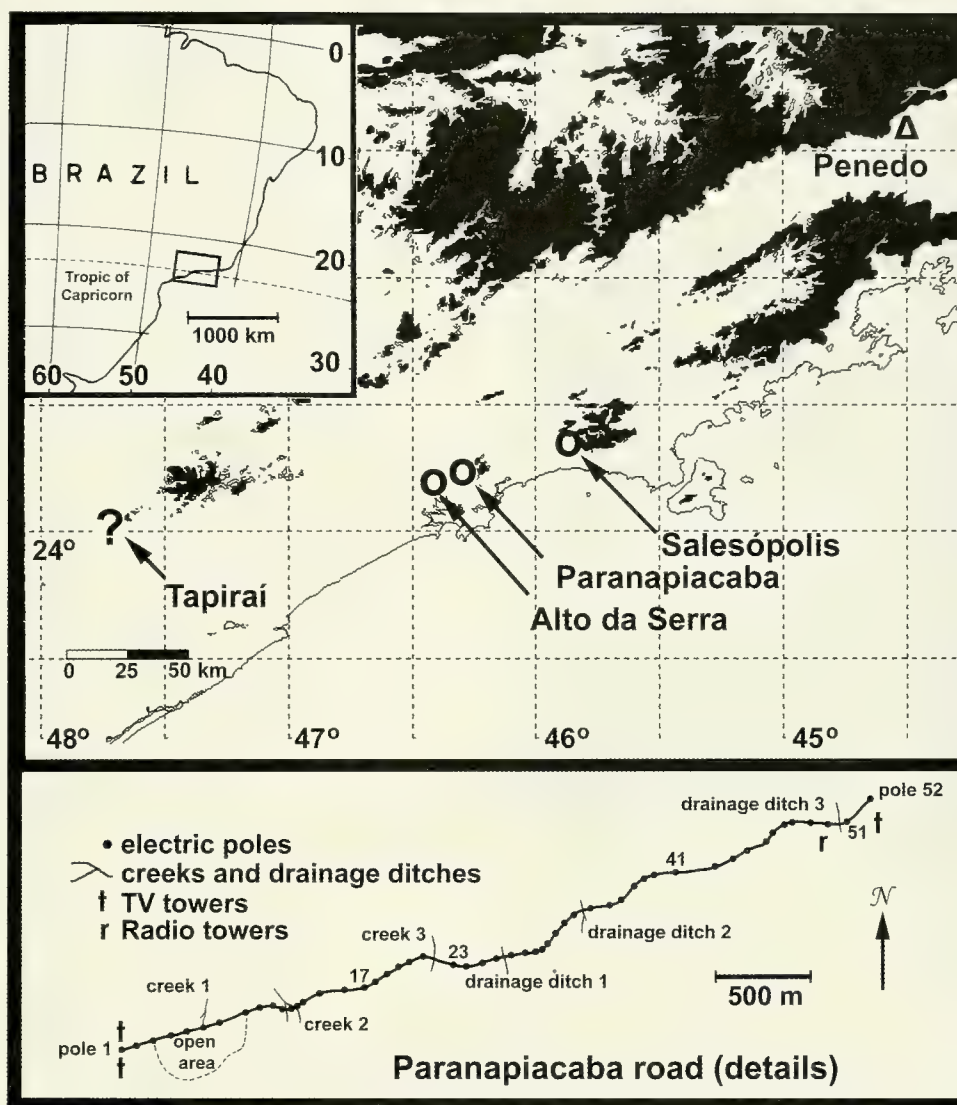


FIG. 1. Study area in Southeastern Brazil (modified from IGGSP 1972a). In the regional map, open circles show the known present and past collecting sites of *A. zikani*; the question mark indicates a doubtful record and the triangle is a locality with a possible undescribed subspecies of *A. zikani*. Black areas indicate altitude above 1000m.

always maintained. The road was mapped with the aid of a tape measure and a compass using a 1:50,000 topographic chart (IGGSP 1972). All 52 electric poles along the road were numbered, permitting the location of each butterfly to be recorded to the nearest 50 m.

The study area is in the rainiest part of Brazil outside of the upper Amazon. The mean annual rainfall between 1870 and 1939 was over 3500 mm, with a minimum of 2355 mm in 1874 and a maximum of 5563 mm in 1872 (NOAA 1998). Data from SIGH (2003) show that the mean annual rainfall between 1936 and 1996 was 3164 mm, with an extraordinary minimum of 826 mm in 1990 and a maximum of 4739 mm in 1947.

The rains roughly occur 15% in winter (June–September), 25% in spring, 35% in summer and 25% in autumn (Santos 1965). Fog is frequent in the study site, and a sunny day could suddenly change to misty and rainy.

The original vegetation is montane rain forest (Ururahy et al. 1984). On the edge of the road above 1000m, there are many patches of bamboos, and "manacá-da-serra", "quaresmeira" (*Tibouchina* spp.; Melastomataceae), and the vine *Mikania hirsutissima* (Asteraceae) are abundant. The trunks and stems of most plants are covered by various epiphytic mosses and ferns. In this area 16 species of Asteraceae were found

which could be potentially used as foodplants by larvae of *Actinote* spp. (RBF unpublished results).

After the discovery of the population of *A. zikani* near Paranapiacaba in 1991, 48 trips were made to the study area up through June 2004 (161 hours of field work); 24 days from January to December 1991 (1-180 days interval), 14 days from July to November 1993 (1-40 days interval) and 10 days in March-June 1994 (1-20 days interval). Butterflies were observed with binoculars and various aspects of behavior were photographed; some individuals were collected for morphological study. All material including the reared specimens was deposited in the collection of the MZUSP.

This population was studied by a mark-release-recapture method (MRR). Each captured individual received a small numbered circle of impermeable paper glued to the ventral base of the left hindwing. This marking technique permits rapid marking and data retrieval; it was previously tested by RBF and used in a population study of *Actinote pellenae pellenae* Hübner in 1988, *Actinote mamita mitama* (Schaus) in 1990, and *Stalactis phlegia susanna* (Fabricius) (Riodinidae) in 1992 (RBF, unpublished data). For each marked butterfly, sex, "age" (based on wing wear), forewing length, location and the time of day were recorded (as in Freitas 1993, 1996). The relative daily abundance was obtained dividing the total number of males sighted by minutes of observation effort, later transformed to butterflies per hour (based only on days with weather conditions favorable for the flight of the butterflies). The MRR data for the summer 1993 generation (12 field days, 1-7 days interval) was analyzed by the Lincoln-Petersen-Bailey method (Southwood 1971) for estimating population parameters (software developed by RBF, UNISANTOS). In most cases, only males were analyzed because of the low number of females recorded. Daily results were tabulated as "number of individuals captured per day" (NICD), and "number of individuals present per day" (NIPD), following Ramos & Freitas (1999). To estimate the NIPD, recaptured individuals were considered to be present in the population on all previous days since the day of first capture. Numbers of reared lots are sequential in the RBF data bank.

RESULTS

Geographic distribution. All known present and past colonies of *A. zikani* are found in a limited area between Salesópolis and Paranapiacaba (São Paulo): Alto da Serra de Santos (a partly unknown spot that could include part of Paranapiacaba), Paranapiacaba and the Estação Biológica de Boracéia (Salesópolis)

(Fig. 1). There is also a mention of this species occurring in southern Minas Gerais (D'Almeida 1951). In November 1991, a male *Actinote* with whitish color pattern was collected by the authors in Penedo, Rezende (Rio de Janeiro), in the foothills of the Serra do Itatiaia. Although the genital armature of this individual is similar to that of *A. zikani*, more material will be necessary to confirm the status of the specimen from Penedo.

Flight activity. The flight activity of *A. zikani* is variable and dependent on weather conditions. Butterflies usually start to fly at approximately 0800 h, when direct sunlight reaches the forest (the summits to the southeast are higher and shade the study area before this time); they open and shut their wings in direct sunlight, basking in a cyclic process until the beginning of flight. On warm but moist days, the flight activity diminished shortly after the sun was covered by clouds. On 20 March 1991, the peak of activity was around 0830 - 0900 h, which was the warmest period of the day (Fig. 2). Males usually fly more than 2 m above the ground along the road, and in forested areas they usually fly above the canopy. Males attack any flying insect that gets less than 1 m from them, when they quickly go up to almost 10 m above the ground or rapidly cover a linear transect of more than 100 m. The relatively small males of *A. zikani* were seen to persecute butterflies as large as *Morpho hercules* (Dalman) (Nymphalidae:

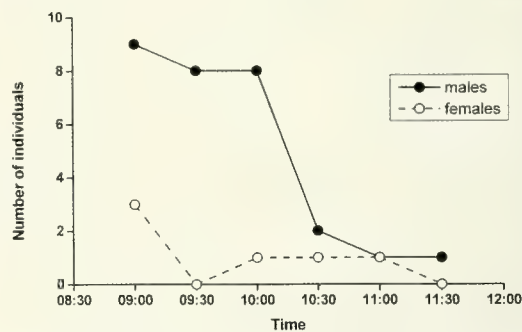


FIG. 2. Flight activity of *A. zikani* in Paranapiacaba, SP, in March 20, 1991, in the area between poles 50 and 51.

Morphinae).

Mating. Mating in *A. zikani* occurs without any apparent courtship display. The patrolling male follows a female; after flying 2 to 5 m in a straight line about 2 m above ground they make a spiraled flight to the ground, at the end of which the male grasps her abdomen with his valves, forcing copulation on the ground ($n = 5$). There is always formation of a plug (sphragis) in the female (as in other *Actinote* species), but in *A. zikani* it is mostly internal and inconspicuous, similar to that

known in *A. discrepans* D'Almeida. Attempts to copulate are sometimes unsuccessful, but once it occurs, it can last more than 30 minutes. On 17 November 1993 a mating pair observed at 0830 h continued "in copula" until at least 0908 h when RBF left the area.

Foraging activity. Feeding activity of adults occurs in the coolest hours of the day, soon after sunrise or before sunset. In the March-April generation of 1991 and 1994, the males were observed drinking nectar from the inflorescences of *Mikania triphylla* (Fig. 3), *Mikania micrantha*, *Eupatorium gaudichaudianum* (Asteraceae), *Mitracarpus hirtus* and *Borreria verticillata* (Rubiaceae). All these food resources were very scarce during the study period, especially in 1994. In the November generation the main nectar sources were two species of myrtaceous trees (*Myrcinia*) that were common along the road. The presence of butterflies was directly related to food resources, with more butterflies present in places with more flowers. On some occasions (cloudy days) females were observed on the ground, or on petals of "manacá-da-serra" (*Tibouchina* sp., Melastomataceae) or large flowers of the exotic "lírio-do-brejo" (*Hedychium coronarium*, Zingiberaceae). In these situations, they appeared to be drinking the accumulated water.

Larval foodplant. The larval foodplant of *A. zikani* is *Mikania obsoleta* (Vell.) G. M. Barroso, discovered after observation of two ovipositing females on 1 April 1991. This is the only hostplant of *A. zikani* known in the study site (from a total of 13 species of *Mikania* present there). *M. obsoleta* was not observed being used by any additional species of *Actinote*. This plant is a climber with halberd-shaped smooth leaves (Fig. 3). It grows around tree trunks climbing to 6 m height. Most individuals of *M. obsoleta* grow near small creeks, in places with wet soil in open canopy areas. The growth of *M. obsoleta* (measured by the number of new leaves) was relatively slow compared with that of other *Mikania* species in the area (e.g. *M. hirsutissima*) (RBF unpublished results). Flowering occurs from October to November and the flowers were not observed attracting any butterflies. A program of monitoring the hostplants revealed that many individuals of *M. obsoleta* tagged in November 1993 had disappeared by April 1994. More than 20 plants disappeared after cleaning of the rivulets (area between poles 16-17) and near creek 1, but some plants inside the forest on the borders of creek 3 also disappeared without any sign of human action.

Oviposition behavior. Females of *A. zikani* had an oviposition behavior similar to that observed in other *Actinote* species (Francini 1989). The female flies



FIG. 3. Above - a male *Actinote zikani* drinking nectar from flowers of *Mikania triphylla*. Below - Close-up view of plant of *Mikania obsoleta* showing details of the halberd shaped leaf and the inflorescence.

around the foodplant landing briefly on some leaves, and after choosing a leaf it lands on its ventral surface. After a period of inactivity (1-5 min) the female starts ovipositing, continuing for up to one hour. On 1 April 1991, five ovipositions were observed in the study area, including one leaf with a double oviposition (two different females observed ovipositing together, lots F-2337 and F-2338). Oviposition in the laboratory was also obtained with a female in a glass jar with a piece of foodplant under a 150W incandescent light bulb (following Francini 1989 and Freitas 1991) (oviposition lot F-2361). In this case, the entire process lasted five hours with the female constantly vibrating her wings. In 1993 only one oviposition was found on a plant inside the forest near a creek, and in 1994 no oviposition was observed in the study area.

Immature development and behavior. Detailed descriptions of the life cycle of *A. zikani* will be presented in a further paper (RBF in prep.). Eggs of a double oviposition collected in the field on 1 April 1991 (F-2337 and F-2338) hatched on 15 April 1991 in laboratory conditions. First instar larvae of *A. zikani* left

the egg after eating the lateral walls of the chorion, leaving the remainder of the egg intact. Feeding activity started after 3-5 hours, and small larvae ate only the ventral epidermis. The fecal pellets were glued onto the leaf by silk, not falling to the ground. There was no significant difference between the mean duration of the larval periods for males (72.5 days, SD = 2.76, $n = 16$) and females (73.6 days, SD = 2.68, $n = 12$) ($t = -1.0414$, $P = 0.30$, DF = 26), nor between the mean duration of the pupal periods for males (mean = 17.2 days, SD = 1.41; $n = 16$) and females (mean = 16.9 days, SD = 0.94, $n = 12$) ($t = 0.4473$; $P = 0.66$, DF = 26). In laboratory conditions, the larvae hatched on 15 April 1991 reached the last instar at the beginning of June; pupation occurred at the end of June and adults emerged in August (almost two months earlier than the flight period in the field). The mean total duration of the life-cycle in the laboratory (egg to adults) was 105.7 days (SD = 3.92, $n = 28$) or roughly three and half months. Trips to the field during all these months showed absence of adults before November. The same life-cycle pattern was observed in 1993 and 1994.

Chemical protection and predation. Qualitative tests for cyanogenesis (following Francini 1989) were done with one male, five eggs, two first instar, and one last instar, and all were positive as for other known species of Neotropical Acraeinae (Brown & Francini 1990). In the field, one oviposition (F-2342) was observed being partially eaten by ants of the genus *Pheidole*. Additionally, a dead male was observed in a web of *Nephila clavipes* (Arachnida: Araneida). No predation on larvae and pupae were observed in the field.

Population biology. Four generations of *A. zikani* were followed between March 1991 and April 1994. Adults of *A. zikani* are bivoltine, with flight periods of about one month; the first generation occurs in March/April (autumn generation) and the second in November (summer generation). In 1991, the autumn generation flew from 16 March to 17 April, and the summer generation from 7 November to 24 November. In 1993 the summer generation flew from 1 November to 28 November, and in 1994 the autumn generation flew from 19 March to 4 April.

The number of butterflies sighted per hour (BSH) varied between 3 and 8 (mean = 5.05, SD = 2.39) in the March-April generation of 1991, between 1 and 17 (mean = 5.33, SD = 4.81) in the November generation of 1993 (Fig. 4) and between 13 and 20 (mean = 14.85, SD = 2.98) in the March-April generation of 1994.

Of the 190 males captured and marked in November, 1993 only 10 (5.3%) were recaptured. Eight individuals were recaptured once, and two individuals were

recaptured twice. In March-April, 1994, due to the unfavorable weather conditions, 35 males were marked and only two recaptured (5.7%). In November 1993, males started to fly on 1 November and females only on 6 November. Both sexes reached highest numbers from 12 - 18 November, after which the population diminished to low numbers until disappearing before the beginning of December (Fig. 4). The number of individuals present per day (NIPD) in the summer 1993 generation varied from 1 to 48 (mean = 18.3, SD = 15.5, $n = 11$ days) (Fig. 4). The estimated population size based on Lincoln-Petersen-Bailey in November 1993 showed that population peaks can include more than 1000 males in the study site (Table 1).

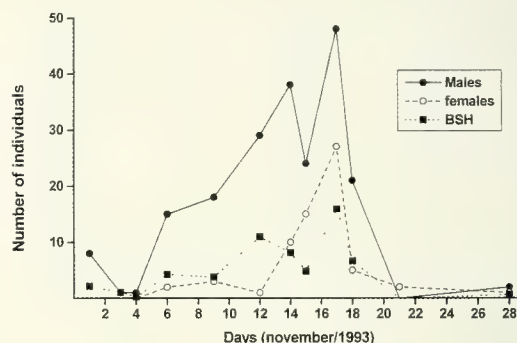


FIG. 4 - Number of individuals present per day (NIPD) for males (solid circles) females (open circles) and number of butterflies sighted per hour for males (BSH solid squares) in November 1993 in Paranapiacaba, SP.

Sex ratio. The sex ratio in the field was male biased in all study periods (Table 2), with lowest male:female ratios in November 1993. In the laboratory, the sex ratio was not different from 1:1 (Table 2). In the November 1993 generation, males were the dominant sex in all but one day with more than 15 individuals (Table 1).

Age structure and residence time in 1993. Most of the first captures of both sexes were individuals of "intermediate" age (59% of males and 63% of females). The age structure in November 1993 shows a clear pattern of individuals becoming older from the beginning to the end of flight period (Fig. 5). Residence time for males ranged from two to six days, with six males lasting two days, three males lasting three days and a single male lasting six days (mean = 2.7 days, SD = 1.25; $n = 10$). A single female was recaptured during the study, with a residence of 10 days.

Vagility. The average distance traveled by males in 1993 was 232.3 meters (SD = 287.9; $n = 17$), not significantly different of that of females (mean = 136.7

TABLE 1 - Summary of population data for the summer 1993 generation of *Actinote zikani* in Paranapiacaba, SE Brazil. NICD = number of individuals captured per day, M = males, F = females; NIPD = number of individuals present per day (males only), BSH = butterflies sighted per hour (males only) rounded off to nearest integer, LPB - number of butterflies estimated by Lincoln-Petersen-Bailey, SE - standard error. An asterisk indicates a male biased sex ratio (chi square test [χ^2], $p < 0.05$).

Date	NICD		Sex ratio	NIPD	BSH	LPB	SE
	M	F					
1993							
01/NOV	8	0	—	8	2	8	—
03/NOV	1	0	—	1	1	1	
04/NOV	1	0	—	1	1	16	21
06/NOV	14	2	7:1°	15	4	142	142
09/NOV	18	3	6:1°	18	4	270	295
12/NOV	29	1	29:1°	29	11	157	98
14/NOV	31	10	3:1°	38	8	444	481
15/NOV	22	15	1.5:1	24	5	1104	1514
17/NOV	45	27	1.7:1°	48	16	1034	366
18/NOV	20	5	4:1°	21	7	63	8
21/NOV	0	1	—	0	0	—	—
28/NOV	2	1	—	1	1	—	—

TABLE 2 - Sex ratio of marked and reared *Actinote zikani* from Paranapiacaba, SE Brazil. An asterisk indicates a male biased sex ratio (chi square test [χ^2], $p < 0.001$).

	Males	Females	Sex ratio	χ^2
Field captures —				
Autumn 1991	50	11	4.5:1	24.9°
Summer 1993	190	65	2.9:1	61.3°
Autumn 1994	35	2	17.5:1	23.5
Reared material				
Lot 2337	3	3	1:1	—
Lot 2338	13	9	1.4:1	0.727

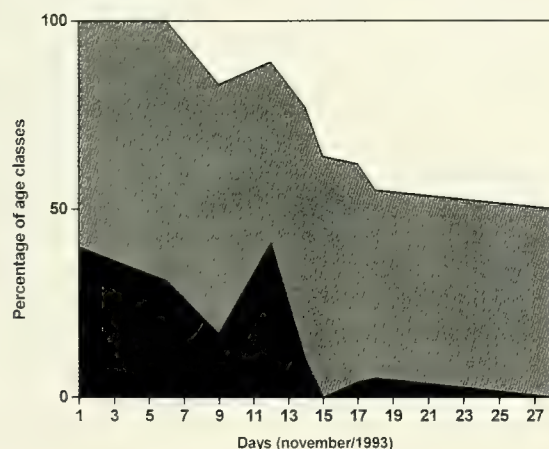


FIG. 5. Age structure of *Actinote zikani* in Paranapiacaba, Santo André, SP, in November 1993. Black = fresh individuals, gray = intermediate individuals, white = old individuals as % of each day's captures.

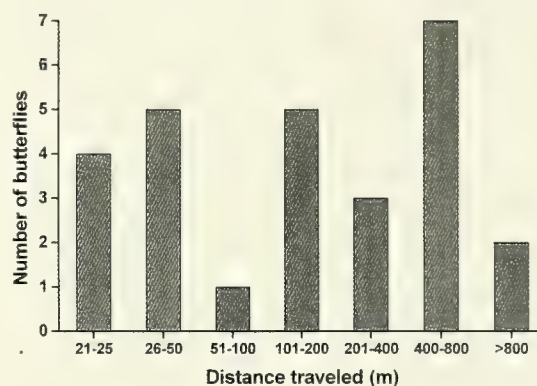


FIG. 6. Maximum distances traveled by *Actinote zikani*, using MRR data from generations of November, 1993 and March, 1994 in Paranapiacaba, SP.

meters; SD = 195.0; $n = 3$) ($t = -0.5474$, $P = 0.59$, $DF = 18$). Individual butterflies were recaptured up to 1000 m from their marking point. On 6 April 1991 a female of *A. zikani* was collected flying in a straight line in a westward direction along the road to Paranapiacaba, about 4 km from the study area. Fig. 6 shows the vagility of *A. zikani* based on data from summer 1993 and autumn 1994.

Adult size. Based on sampled individuals from March-April 1991, the forewing length of females (mean = 37.14 mm, SD = 2.575, $n = 64$) was greater than that of males (mean = 32.88 mm, SD = 2.539, $n = 197$) ($t = 12.281$, $p < 0.05$, $DF = 259$). In the same period, the dry weight of males varied from 0.30 to 0.48g (mean = 0.41g, SD = 0.052, $n = 10$), and the dry

weight of the females varied from 0.65 to 0.89g (mean = 0.74g, SD = 0.098, $n = 5$), showing that even though females weighed almost twice as much than males, the length of their forewing was only 1.1 times greater. Adults of *A. zikani* are large, compared with other species in the genus *Actinote* (RBF unpublished data).

DISCUSSION

Natural History and Population Biology. In most aspects of population biology and natural history, *A. zikani* is similar to the other known species of *Actinote* from SE Brazil. The bivoltinism is characteristic of most known species of *Actinote*, except *A. pellenea* and *A. brylla* Oberthür, that can be multivoltine in warm places, and most red species in the "red mimicry complex" that are univoltine (Francini 1989, 1992, Penz & Francini 1996). The adult permanence in the population of less than one week is low if compared with most neotropical butterflies (Ramos & Freitas 1999), but it is similar to the values obtained for most species of *Actinote* (Francini 1989 and unpublished data). These low values are suggested as a combination of short lifespan and high dispersal rates in these butterflies (Francini 1989). Even if flight periods and time intervals (about one month) are similar to the duration of generations of other *Actinote* species (Francini 1989), there is an asynchrony of *A. zikani* with relation to other *Actinote* species of about one month. During the present study, other species of *Actinote* like *A. canutia* (Hopffer), *A. carycina* Jordan, *A. parapheles* Jordan, *A. melanisans* Oberthür and *A. genitrix* D'Almeida began to fly in Paranapiacaba only in the middle of April in the autumn generation (*A. zikani* started in early March). It is interesting to note that the labels of Museum specimens (April 1941 and December 1931) contributed to the delay in finding the species, since much time was spent in the field 20-30 days after the flight period of *A. zikani*. The male biased sex ratios recorded for *A. zikani* in the field are similar to those of the other 13 species of *Actinote* from SE Brazil (Francini 1989). Male biased sex ratios are usually observed in butterflies in the field even if laboratory broods are 1:1 (Brussard & Ehrlich 1970, Freitas 1993, 1996, Ramos & Freitas 1999). The recapture rate of about 5% recorded for *A. zikani* is low even if compared with those of other species of *Actinote* (Francini 1989). Francini (1989) recorded recapture rates of 12% and 8% for *A. pellenea pellenea* and *A. brylla* Oberthür, 1917 respectively in the coastal plain of São Paulo.

General features of the immatures conform to those of other species of *Actinote* (Francini 1989, 1992). The host plant agrees with the suggestion of D'Almeida

(1951) who proposed that the host plant of *A. zikani* should be a species of *Mikania*. Immatures of *A. zikani* are gregarious like all other known Neotropical Acraeinae (Francini 1989), and the presence of a double oviposition (two different ovipositions in the same leaf) is also observed in other species that apparently have gregarious ovipositing (Francini & Freitas unpublished data). The pattern of lateral eclosion differs from all other known *Actinote*, whose larvae exit through the micropylar region (Francini 1989). Maybe the most remarkable feature is the fast development of immatures in laboratory conditions; only three and half months without periods of diapause or slow growing. Even though the larvae were reared under temperature conditions ($25^{\circ}\text{C} \pm 2^{\circ}\text{C}$) different from those in the field (that can be near 0°C on some winter nights), the duration of the larval stage in *A. zikani* was exceptionally short for an *Actinote* species, except for some broods of *Actinote pellenea pellenea* that were reared in summer at sea level (about two months, Francini 1989 and unpublished data). This capacity to grow quickly at high temperatures could be an indication that any *Actinote* could be multivoltine if conditions are adequate.

Conservation of *A. zikani* and its habitats. The conservation status of *A. zikani* was defined as critically endangered in the most recent evaluation of the Brazilian list of endangered species (MMA 2003), based on a combination of: restricted area of occupancy, few known and declining populations and sites, small total population size and extreme fluctuations in number of mature individuals (categories B2 bii, iii, iv c Cb - criteria from IUCN 2001). Only one colony is known at present (this paper); based on museum specimens there are at least two other possible sites where *A. zikani* has occurred (see Fig. 1). Undoubtedly, there is an urgent need for discovering more colonies of this species in the region. The analysis of topographic charts (1:50,000) between Paranapiacaba and Boracéia revealed 10 areas with altitude from 1100 to 1200 m, within 10 km from the Serra do Mar break, all potentially suitable for a population of *A. zikani*. Visits to some of these areas should be an immediate priority. Further areas SW of Paranapiacaba should also be visited; although winter temperatures are lower towards the south (Nascimento & Pereira 1988; Nimer 1972, 1989) little is known about the tolerances of this species and the potential occurrence on both NW- and SE-facing summits. In any case, if there is still a population present in the Estação Biológica de Boracéia, or in any additional location northward, it will be partially isolated from the population studied in Paranapiacaba, since much of the original forest throughout this region has been replaced by eucalyptus trees.

Even the colony of Paranapiacaba is not completely protected. The area is constantly visited for maintenance of the towers, resulting in clearing of the roads and of the drainage network, leading to vigorous growth of more aggressive *Mikania* species that overcome *M. obsoleta*. The heavy ecotourism in the region contributes to environmental degradation and accumulation of garbage in the initial part of the area. The entire ridge of the Serra do Mar area including the region of Paranapiacaba is discontinuous to the southwest, where two major superhighways, two railroads, many oil ducts and service roads, several cleared tracks for power line maintenance, and increasing urbanization of the slopes of the mountains (below 400 m) create a mosaic of unsuitable habitats.

Perhaps due to the extensive and continuous modification of the vegetation in the entire region, recent trips to the area (1997 to 2005) showed no trace of *A. zikani* and few plants of *M. obsoleta*. This microsystem appears to be composed of fugitive species (cf. Horn & MacArthur 1972) which compete poorly with relatives better adapted to this patchy environment (see the example of *Heliconius nattereri* Felder & Felder in Santa Teresa, Espírito Santo in Brown 1972). Nowadays the area seems apparently less impacted (with a single new tower constructed there), but the food plants (*M. obsoleta*) continue to disappear.

The history of environmental conservation in the area of the Serra do Mar in the State of São Paulo starts at the beginning of twentieth century, when Herman von Ihering, director of the Museu Paulista (now Museu de Zoologia da Universidade de São Paulo) demonstrated the need to create federal legislation to regulate bird hunting (Ihering 1902), and later emphasized the conservation of forests (Ihering 1911). At the end of 1909 he set up on his own property a sanctuary, the "Estação Biológica do Alto da Serra", now under responsibility of the Instituto de Botânica da Secretaria da Agricultura do Estado de São Paulo (Kirizawa et al. 2004). This protected area is located SW of Paranapiacaba, and unfortunately has been heavily polluted with fluoride and other chemical contaminants from the Cubatão industrial area at the base of these mountains (Klump et al. 1996; Kirizawa et al. 2004).

Future perspectives. The observations made here are an initial step to a better understanding of this fugitive pair of species *A. zikani* and *M. obsoleta*. To help answer the open questions, the following actions are needed: more accurate estimates of population parameters (mean residency time and home-range), verification of the impact of the ants that prey on eggs, better estimates of population parameters of the foodplant, and laboratory testing of larval acceptance of

other *Mikania* species. In spite of the study site being close to a contaminated area (see above), the population of *A. zikani* is relatively protected against air pollution by the summits of a nearby mountain range, that deflect the winds toward the west.

The reasons for the observed disappearance of the population in the study area (see above) were not investigated. Perhaps there is a natural cycle of this pair of species, becoming common in a few years and scarce in most (as observed for some species of *Actinote* by the authors).

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LITERATURE CITED

- BERNARDES, A. T., A. B. M. MACHADO & A. B. RYLANDS. 1990. Fauna brasileira ameaçada de extinção. Fundação Biodiversitas/IBAMA, Belo Horizonte, 60 pp.
- BROWN, K. S., JR. 1972. The *Heliconius* of Brazil (Lepidoptera: Nymphalidae). Part III. Ecology and biology of *Heliconius nattereri*, a key primitive species near extinction, and comments on the evolutionary development of *Heliconius* and *Eueides*. *Zoologica*, 57: 41-69.
- . 1991. Conservation of Neotropical environments: insects as indicators, pp. 349-404. In Collins, N. M. & J. A. Thomas (eds.). *The Conservation of Insects and their Habitats*. Academic Press, London.
- BROWN, K. S., JR. & R. B. FRANCINI. 1990. Evolutionary strategies of chemical defense in aposematic butterflies: cyanogenesis in Asteraceae-feeding American Acraeinae. *Chemoecology*, 1: 52-56.
- BRUSSARD, P & P. R. EHRLICH. 1970. The population structure of *Erebia epipsodea* (Lepidoptera: Satyrinae). *Ecology*, 51: 119-129.
- D'ALMEIDA, R. F. 1943. Algumas observações sobre o *Actinote morio* Oberthür, 1917 (Lep. Heliconidae, Acraeinae). *Papéis Avulsos do Departamento de Zoologia*, São Paulo, 3: 107-110.
- . 1951. Uma nova espécie de *Actinote* do Sul do Brasil (Lep. Heliconiidae, Acraeinae). *Arquivos do Museu Nacional*, Rio de Janeiro, 42: 1-5.
- FRANCINI, R. B. 1989. Biologia e ecologia das borboletas *Actinote* (Lepidoptera, Nymphalidae, Acraeinae) na transição subtropical no sudeste do Brasil. Dissertação de Mestrado em ecologia, Universidade Estadual de Campinas. 236 pp.
- . 1992. Ecologia das taxocenoses de *Actinote* (Lepidoptera: Nymphalidae) em Asteraceae (Angiosperma: Magnoliatae) no sudeste do Brasil: subsídios para conservação. Tese de doutoramento em ecologia, Instituto de Biologia, Universidade Estadual de Campinas, SP, 194 pp.
- FREITAS, A. V. L. 1991. Variação morfológica, ciclo de vida e sistemática de *Tegosa claudina* (Eschscholtz) (Lepidoptera, Nymphalidae, Melitaeinae) no estado de São Paulo, Brasil.

- Revta. bras. Ent. 35: 301-306.
- . 1993. Biology and population dynamics of *Placidula euryanassa*, a relict ithomiine butterfly (Nymphalidae: Ithomiinae). J. Lepid. Soc. 47: 87-105.
- . 1996. Population biology of *Heterosais edessa* (Nymphalidae) and its associated Atlantic Forest Ithomiinae community. J. Lepid. Soc. 50: 273-289.
- HORN, H. S. & R. H. MACARTHUR. 1972. Competition among fugitive species in a harlequin environment. Ecology, 53: 749-752.
- IGGSP (editor) 1972. Folha SANTOS, SF-23-Y-D-IV-4. Mapa topográfico em escala 1:50.000. Instituto Geográfico e Geológico do Estado de São Paulo, São Paulo.
- IHERING, H. 1902. Necessidades de uma lei federal de caça e proteção de aves. Revista do Museu Paulista, 5: 238-260.
- . 1911. Devastação e conservação das matas. Revista do Museu Paulista, 8: 485-500.
- IUCN 2001. IUCN Red List Categories and Criteria version 3.1. IUCN, Gland and Cambridge.
- KIRIZAWA, M., M. SUGIYAMA, E. A. LOPES & A. CUSTODIO-FILHO. 2004. Flora da Reserva Biológica do Alto da Serra de Paranapiacaba Santo André, São Paulo, Brasil. http://www.ibot.sp.gov.br/PESQUISA/paranapiacaba/paranapi_resultados.htm
- KLUMPP, A., M. DOMINGOS & G. KLUMPP. 1996. Assessment of the vegetation risk by fluoride emissions from fertiliser industries at Cubatao, Brazil. The Science of Total Environment, 192: 219-228.
- LAMAS, G. 1973. The type material of Lepidoptera Rhopalocera contained in the collections of the Museu de Zoologia da Universidade de São Paulo. Papéis Avulsos de Zoologia, São Paulo, 26: 179-185.
- MIELKE, O. H. H. & M. M. CASAGRANDE. 1986. Sobre os tipos de Lepidoptera depositados em museus brasileiros. III. Nymphalidae (Danainae, Brassolinae, Morphinae, Satyrinae e Acraeinae), descritos por R.F.D'Almeida. Revista Brasileira de Entomologia, 30: 141-152.
- MMA, 2003. Anexo à Instrução Normativa nº 3, de 27 de maio de 2003, do Ministério do Meio Ambiente. Lista das Espécies da Fauna Brasileira Ameaçadas de Extinção. <http://www.ibama.gov.br/fauna/downloads/lista%20spp.pdf>
- NASCIMENTO, C. M. & M. A. M. G. PEREIRA. 1988. Atlas climatológico do Estado de São Paulo. Fundação Cargill, Campinas.
- NIMER, E. 1972. Climatologia da região sudeste do Brasil. Introdução à climatologia dinâmica. Revista Brasileira de Geografia, Rio de Janeiro, 34: 3-48.
- . 1989. Climatologia do Brasil. Fundação IBGE, Rio de Janeiro, 421 pp.
- NOAA 1998. The Global Historical Climatology Network (GHCN). http://www.ncdc.noaa.gov/oa/pub/data/ghcn/v2/ghcnftp_zipd.html
- PENZ, C. M. & R. B. FRANCINI. 1996. New species of *Actinote* Hübn. (Nymphalidae: Acraeinae) from Southeastern Brazil. Journal of the Lepidopterists' Society, 50: 309-320.
- RAMOS, R. R. & A. V. L. FREITAS. 1999. Population biology and wing color variation in *Heliconius erato phyllis* (Nymphalidae). J. Lepid. Soc. 53: 11-21.
- SANTOS, E. O. 1965. Características climáticas, pp. 95-150. In Azevedo, A. (ed.). A baixada Santista, aspectos geográficos, vol. 1. Cia. Editora Nacional/EDUSP, São Paulo.
- SIGRH. 2003. Sistema Integrado de gerenciamento de recursos hídricos do Estado de São Paulo: Banco de dados Pluviométricos do Estado de São Paulo. <http://www.sigrh.sp.gov.br/sigrh/basecon/bancodedados/plu/plu.htm>
- SOUTHWOOD, T. R. E. 1971. Ecological Methods with Particular Reference to the Study of Insect Populations. Chapman & Hall, London, 524 pp.
- SP-SMA. 1998. Fauna ameaçada no estado de São Paulo. Secretaria do Meio Ambiente, SMA/CED, São Paulo.
- URURAHY, J. C. C., J. E. R. COLLARE S, M. M. SANTOS & R. A. A. BARRETO. 1984. 4. Vegetação, pp. 553-611. In Projeto RADAMBRASIL, levantamento de Recursos Naturais. Vol. 32. fls. Sf 23-24 (Rio de Janeiro e Vitória). Fundação IBGE, Rio de Janeiro

EXTRINSIC EFFECTS ON FECUNDITY-MATERNAL WEIGHT RELATIONS IN CAPITAL-BREEDING LEPIDOPTERA

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ABSTRACT. Capital-breeding Lepidoptera depend for reproduction on metabolic resources assembled either entirely or primarily by their larvae, the former termed 'perfect' the latter 'imperfect'. Empirical evidence suggests that maternal size determines capital-breeder fecundity. The fecundity-maternal size relation is usually formulated as $F = bW + a$, where F is fecundity, W is final maternal size in units such as weight of newly transformed pupae, b is the slope, and a the intercept. Exhaustive search yielded 71 fecundity-maternal pupal weight relations for 41 capital breeders in 15 families, 58 of which, including 2 previously unpublished, were based on individual specimens, and 13 on grouped specimens. In 22 individual-specimen relations, cohorts divided into 2 or more subgroups were reared simultaneously at different temperatures, on different diets, or exposed to other extrinsic factors. These 22 'multiform' relations were compared with 36 'uniform' relations, and where possible cohort subgroups were compared. Pupal weights of cohort subgroups were affected much oftener than underlying slopes and intercepts. Individual-specimen slopes based on transformed data ranged 0.52–2.09 with a mean and standard error of 1.13 ± 0.04 , and slopes did not differ significantly among perfect, imperfect, multiform, and uniform categories. Despite the evident similarity, one relation does not apply to all capital breeders. Tradeoffs sometimes occur between fecundity, F , and mean egg weight, E . Reaction norms of fecundity and pupal weight across extrinsic-factor ranges were overwhelmingly congruent, which supports axiomatic status for the dependence of fecundity on capital-breeder maternal size. Cooler rearing temperatures usually produced heavier female pupae and greater fecundities, a phenomenon of population dynamics interest. The two sides of practically all fecundity-maternal weight regressions are not statistically independent, in effect stating $F = b(W + [F \times E]) + a$, which artificially inflates test statistics. Where desirable, the fully independent relation $R = b(W - [F \times E]) + a$ can be used, where R is reproductive bulk, the mathematical product of $F \times E$.

Additional key words: temperature, diet quality, population dynamics

'Capital-breeding' describes Lepidoptera that depend for reproduction entirely or primarily on metabolic resources assembled by their larvae, in contrast to 'income-breeding', which describes those that depend for reproduction primarily or entirely on resources assembled by their adults (Boggs 1992, Miller 1996, Tammaru and Haukioja 1996). The gypsy moth, *Lymantria dispar* (L.) (Lymantriidae), is a capital breeder; the monarch butterfly, *Danaus plexippus* (L.) (Nymphalidae), an income breeder. In four butterfly income breeders in two families, income contributed $\geq 80\%$ to fecundity, and capital $\leq 20\%$ (Boggs 1997, Fischer and Fiedler 2001a). Based on sizes of superfamilies (Kristensen and Skalski 1999) and the extent to which income breeding is phylogenetically limited, probably $\approx 90\%$ of extant Lepidoptera are capital breeders. Most outbreak Lepidoptera also are capital breeders (Miller 1996, Tammaru and Haukioja 1996). Capital breeders have an ovigeny index, OI, of 1 or $\gg 0$, referring to the proportion of lifetime potential fecundity that consists of mature eggs at eclosion, whereas income breeders have an OI of 0 or $\ll 1$ (Jervis and Ferns 2004). Capital breeders with nonfeeding adults and OIs of 1 are here termed 'perfect', whereas those with OIs of $\gg 0$ whose adults may feed, but do so less than income breeders, are termed 'imperfect'.

Maternal size is widely believed to determine fecundity in capital breeders (Leather 1988, Honek 1993). This belief derives not from experimentation but

from long empirical observation. Direct fecundity-size relations occur in the lepidopteran phylogenetic sequence at least as early as Tineidae, the basal-most lineage of Ditrysia (Titschack 1922, Kristensen and Skalski 1999) and are probably part of the ground plan of Ditrysia, if not all Lepidoptera. This dependence implies that whatever influences maternal size may influence fecundity and its associated quality attributes, and thus population fluctuations. Fecundity can be a proxy for net reproductive rate (Carey 1993, Huey and Berrigan 2001) and has been implicated in capital-breeder population fluctuations, as in *Bupalus piniaria* L. (Geometridae) (Klomp 1966), *Bucculatrix pyrivorella* Kuroko (Bucculatricidae) (Fujiie 1980), *Leucoptera spartifoliella* (Hübner) (Lyonetiidae) (Agwu 1974), and in capital-breeding Noctuidae (Spitzer et al. 1984).

Traditionally, the relation between fecundity, F , and maternal weight, W , usually has been defined by linear regression as $F = bW + a$, where W refers to newly transformed pupae or newly eclosed adults, b is the slope, and a is the intercept or scaling parameter. Honek (1993) devised a fecundity-maternal weight relation for insects generally, as well as one for Lepidoptera, but he did not segregate capital breeders for special study nor exhaustively seek examples. Honek noted that weight appears on both sides of fecundity-maternal weight regressions, but that statistically independent measures of fecundity and maternal weight are practically

nonexistent. In effect, such relations state that $F = b(W + [F \times E]) + a$, where E is mean egg weight. The resulting nonindependence inflates test statistics and minimizes variation between response and explanatory variables. The practical usefulness of the traditional regressions is not necessarily impaired, but their statistics should not be used where strict independence between the variables is assumed. As discussed further on, a fully independent alternative relation emerged from this study.

In any capital-breeder reared under homogeneous conditions, intrinsic effects alone will produce a direct relation between fecundity and maternal size. If a cohort of eggs or hatchlings is divided into subgroups, and each subgroup reared at a different level of an extrinsic factor, such as a different temperature, or on a different diet, then extrinsic effects are likely to be added to the intrinsic ones. Here I examine extrinsic effects on fecundity-maternal pupal weight relations during rearing of capital breeders. I focus on effects produced by different temperatures—as might occur during anomalous weather, or between microhabitats, or between generations or seasons—and by differing diet quality—as might occur on variably stressed or different kinds of foodplants, or on different kinds or amounts of adult nourishment.

MATERIALS AND METHODS

I assembled as many statistical fecundity-maternal weight relations as possible from a personal reference collection, electronic databases including *Biosis*, *Biological Abstracts*, and the *Zoological Record*, and from citations in references. Most relations were based on observations of specimens individually, a few on means of grouped specimens. Individual-specimen relations were admitted if based on samples numbering ≥ 20 , grouped-specimen relations if based on groups numbering ≥ 5 . No relations were excluded because of non-English text.

In the 58 assembled individual-specimen relations, weights and fecundities were available in numerical form for three published and two unpublished ones (Table 1); weights and fecundities for the remainder were transcribed from enlarged photocopies of published scatterplots. Because transcription creates error—when one point covers another, for instance—I tested slopes of transcribed relations against corresponding slopes given in sources. A few departures were statistically significant, but most were not (F -tests, $P = 0.99\text{--}0.009$; median $P = 0.76$; $n = 35$). If P was < 0.25 , I retranscribed, but in no case did retranscription change the outcome appreciably. I accepted scatterplots at face value despite minor inconsistencies, except that

for *Philosamia ricini* Hutt. (Singh and Prasad 1987), which seemed too anomalous. In the 13 grouped-specimen relations, most weights and fecundities were available in numerical form (Table 2).

Study relations consisted of perfect and imperfect groups and uniform and multiform subsets. 'Uniform' denotes homogeneous conditions of development expected to produce only intrinsic effects, and 'multiform' denotes heterogeneous conditions expected to produce extrinsic as well as intrinsic effects. I examined relations for extrinsic effects first by meta-analysis (Gates 2002) and second by comparing cohort subgroup relations provided in sources or obtained by deconstruction.

A standardized maternal weight was desirable, and I chose fresh pupal weight. By the pupal stage metabolic resources for ovigenesis are in place. Moreover, pupal weight has been most often used in describing fecundity-size relations (42 of 58 relations in Table 1, 12 of 13 in Table 2), and explanatory variables based on weight outnumber those based on lineal dimensions such as forewing length and pupal diameter. I maximized the number of relations for study by converting female adult fresh weight, W_a , to fresh pupal weight, W_p , where $W_p = W_a \times 1.85$, a factor based on four observations: (1) first-day female pupae of *Malacosoma disstria* (Hbn.) (Lasiocampidae) in a previously unpublished study averaged 1.98 times heavier than first-day adults ($n = 30$ weighings, paired); (2) a corresponding value of 1.81 for *Epiphyas postvittana* (Walker) (Tortricidae) ($n > 130$ weighings, unpaired) (Danthanarayana 1975); (3) a corresponding value of 1.74 for *Streblote panda* (Hbn.) (Calvo and Molina 2005); and (4) a corresponding value of 1.67 for *Cnephasia jactatana* (Walker) (Tortricidae) (Ochieng'-Odero 1990).

Fecundity had been estimated in sources by various methods, all internally consistent and all accepted here. Methods included counting unlaidd eggs in dissections of newly eclosed females, counting only eggs actually laid, and combining eggs laid with residual eggs in ovaries after death.

For meta-analysis, I transformed fecundities and pupal weights of each relation to percentages of their midranges (Honek 1993) ([individual value/midrange value] $\times 100$, where midrange = $0.5 \times [\text{minimum value} + \text{maximum value}]$). This transformation enabled comparison of relations for different species and groups on a single scale, as between large saturniids and small tortricids.

Statistics were generated by SYSTAT (1992) software. Student's t used pooled variances except where noted otherwise. In analyzing and comparing cohort subgroup

relations, I used nontransformed transcribed data when tabulated data were unavailable. In tests of differences among fecundity-maternal weight regressions of cohort subgroups, I included a categorical explanatory variable, as well as a maternal weight \times group interaction term, the latter enabling tests of differences among slopes and the former enabling tests of differences among heights of regression lines. Height tests were used here as tests of intercept differences. Where subgroup relations within multiform relations were not provided in sources and deconstruction was not possible, the fact is noted.

Wherever possible, I report whether reaction norms of fecundity and maternal pupal weight are congruent. A reaction norm is the trajectory of response values across the range of an extrinsic factor (Schlichting and Pigliucci 1998). Congruency signifies that fecundity and female pupal weight peak at the same value of an extrinsic factor. Reaction norms to rearing temperatures are illustrated in Fig. 1a, and those to different diets in Fig. 2a. In sources where it was not possible to evaluate congruency, it is noted as indeterminate.

RESULTS

The 71 assembled fecundity-maternal pupal weight relations represent 41 capital breeders in 15 families (Tables 1 and 2). The 58 individual-specimen relations (Table 1) consist of 35 in perfect and 23 in imperfect groups, 36 of the 58 uniform and 22 multiform. Perfect-uniform and perfect-multiform categories number 23 and 12, and imperfect-uniform and imperfect-multiform categories each number 13. The 13 grouped-insect relations (Table 2) consist of 10 of the perfect kind and 3 of the imperfect, with 5 uniform and 8 multiform. Individual-specimen relations are unaffected by aggregation bias and thus receive more attention here than grouped-specimen relations. In all discussions, attributes and their numerical values appear in parallel sequences. 'Tradeoffs' refer to any change in proportion between fecundity and egg size. Egg size refers to the mean weight of one egg in an egg load.

Individual-specimen relations

Meta-analysis. Midrange maternal pupal weight, which approximates the mean, varied from 12–9435 mg (Table 1), averaging 1401 and 63 mg for perfect and imperfect groups. The difference is highly significant (Student's t [separate variances] = 3.74; df = 34.1; P < 0.001). Range in transformed weights of pupae (greatest % of midrange minus smallest % of midrange) varied from 34–179 (Table 1), averaging 97 and 99 for perfect and imperfect groups. Corresponding uniform and multiform ranges are 34–179 and 48–143 (Table 1), averaging 97 and 100.

Slopes of fecundity-maternal pupal weight relations varied from 0.52–2.09 (Table 1, Fig. 3), with the mean and standard error, SE, 1.13 ± 0.04 . This overall mean significantly exceeds 1.00 (Student's t [one-tailed test] = 3.02; df = 57; P = 0.02). Slopes for perfect and imperfect groups average 1.14 and 1.12; those for uniform and multiform subsets also 1.14 and 1.12. The four slopes for perfect-uniform and perfect-multiform, and imperfect-uniform and imperfect multiform categories average 1.13 and 1.15, and 1.14 and 1.09. Differences among them are not significant (F = 0.08; df = 3, 54; P = 0.97). Pooled slopes are likewise unrelated to midrange pupal weight (Pearson's r = 0.06; df = 56; P = 0.68) or to range (Pearson's r = 0.04; df = 56; P = 0.77). Although a positive correlation among relations between range and number of observations either as n or $\log_e n$ could be expected statistically, it did not materialize (Pearson's r = 0.16; df = 56; P = 0.24). Slope variability as SE_b/b among perfect-uniform and perfect-multiform categories averaged 9.5 and 8.9, and among imperfect-uniform and imperfect-multiform, 13.0 and 15.7. The mean for the entire imperfect group, 14.8, is seemingly higher than that for the entire perfect group, 9.3, but the difference is not strictly significant (Student's t [separate variances] = 1.85; df = 27.4; P = 0.07). So-called funnel diagrams—plots of SE_b vs. b —visually suggest greater scatter among imperfect than perfect groups (Fig. 3a, b).

Spatial and temporal effects. Coefficients of fecundity-maternal pupal weight relations for the same species often differ geographically (Table 1), but only those obtained in the same way by the same workers can be meaningfully compared, as in the following examples. Lorimer (1979) found slopes and intercepts of two uniform relations for *Malacosoma disstria* from Indiana and Michigan to differ significantly. Parry et al. (2001) found four of the six *M. disstria* slope comparisons for Michigan, Manitoba, and Louisiana between two years to differ significantly, as well as all of the six intercept comparisons. In *M. disstria*, however, a tradeoff between fecundity and egg size occurs as a geographic NW-SE cline (Parry et al. 2001). At two Quebec locations, slopes of 0.26 and 0.18 for *Lymantria dispar* differed significantly (F = 20.5; df = 1, 111; P < 0.001) (transcribed data) (Madrid and Stewart 1981). Egg size is notably plastic in *L. dispar* (Rossiter 1991). Lorimer and Bauer (1983) found that fecundity-pupal weight slopes for *Choristoneura fumiferana* differed between New Hampshire and Minnesota; atypically, significant correlation was absent in the latter (transcribed data). Harvey (1983) demonstrated a geographic NW-SE cline in *C. fumiferana* egg size, as well as a clear geographic tradeoff between fecundity

TABLE 1. Regressions relating fecundity, F_p , to maternal pupal weight, W_p , in capital breeders based on transformed values for individual specimens.

No.	Species	Family	Pupal weight			Equation ($F_p = bW_p + a$)					Source of data	
			Midrange (mg)	Min. (%)	Max (%)	Range (%)	b, SE	a	r ²	n		
Perfect-uniform												
1.	<i>Callosamia promethea</i> (Drury)	Saturniidae	1488	45	155	110	1.11, 0.06	-18.6	0.94	25	Miller et al. 1983	
2.	<i>Antheraea polyphemus</i> (Cramer)	"	2760	46	154	108	0.73, 0.12	14.6	0.62	26	Miller et al. 1982	
3.	<i>A. assamensis</i> Helfer	"	7255	83	117	34	1.25, 0.10	-22.5	0.88	24	Yadav & Goswami 1999	
4.	<i>A. paphia</i> (L.) ^a	"	9435	74	126	52	1.00, 0.24	-6.4	0.45	23	Yadav et al. 2001	
5.	<i>Nudaurelia c. cytherea</i> (F.)	"	5800	59	143	84	1.32, 0.34	-38.0	0.41	24	Geertsema 1975	
6.	<i>Latoia viridissima</i> Holland ^a	Limacodidae	562	38	122	84	1.30, 0.07	-40.9	0.79	95	Igbinosa 1992	
7.	<i>Epirrita autumnata</i> (Bkh.)	Geometridae	70	46	154	108	1.29, 0.09	-51.5	0.66	100	Haukioja & Neuvonen 1991	
8.	<i>Bupalus piniaria</i> (L.)	"	138	65	134	69	0.76, 0.12	0.7	0.19	157	Stahl 1939	
9.	<i>B. piniaria</i> ^b	"	115	61	139	78	1.40, 0.12	-48.3	0.67	70	Bevan & Paramonov 1957	
10.	<i>Operophtera brumata</i> (L.) ^a	"	49	23	196	173	1.26, 0.09	-22.7	0.76	58	Kikuzawa et al. 1979	
11.	<i>O. brumata</i> ^a	"	44	10	189	179	1.22, 0.06	-38.8	0.85	74	Holliday 1977	
12.	<i>Lymantria dispar</i> (L.) ^{a, c}	Lymantriidae	1517	62	138	76	1.88, 0.16	-70.2	0.70	55	Madrid & Stewart 1981	
13.	<i>L. dispar</i> ^{a, d}	"	1957	47	153	106	1.10, 0.02	-10.5	0.98	60	"	
14.	<i>Dendrolimus pini</i> (L.) ^{a, b}	Lasiocampidae	3034	52	154	102	0.81, 0.09	16.2	0.59	58	Eckstein 1911	
15.	<i>Malacosoma dissitria</i> (Hbn.)	IN ^e	300	57	143	86	1.24, 0.10	-15.2	0.76	55	Lorimer 1979	

16.	"	MI	"	358	58	142	84	1.00, 0.11	-7.0	0.62	55	"
17.	"	MI '98	"	494	53	147	94	0.84, 0.05	15.2	0.74	84	Parry et al. 2001
18.	"	MI '99	"	464	69	130	62	0.85, 0.09	19.1	0.77	29	"
19.	"	MB '98	"	496	47	153	106	1.16, 0.05	-7.9	0.85	86	"
20.	"	MB '99	"	490	61	139	78	1.19, 0.09	1.9	0.83	24	"
21.	"	LA '98	"	435	39	161	122	0.84, 0.05	15.4	0.81	70	"
22.	"	LA '99	"	464	69	131	62	1.08, 0.07	-4.6	0.88	29	"
23.	<i>M. neustria testacea</i> (Mots.)		"	468	51	149	98	1.37, 0.11	-26.8	0.74	50	Shiga 1977
Perfect-multiform												
24.	<i>Lymantria monacha</i> (L.)		Lymantriidae	480	33	167	134	1.57, 0.07	-64.1	0.88	71	Zwölfer 1933
25.	<i>L. dispar</i> (L.) ^b		"	1466	34	166	132	1.20, 0.10	-23.8	0.72	52	Maksimovic 1958
26.	<i>L. dispar</i>		"	2180	53	147	94	0.91, 0.05	2.5	0.83	62	Cambini & Magnoler 1997
27.	<i>Orgyia vetusta</i> Bdv.		"	533	55	145	90	1.02, 0.22	-21.8	0.44	28	Harrison & Karban 1986
28.	<i>Euproctis chrysorrhoea</i> (L.)		"	222	47	153	106	1.38, 0.07	-38.5	0.86	56	Van der Linde & Voüte 1967
29.	<i>Malacosoma neustria</i> (L.)		Lasiocampidae	498	58	142	84	1.20, 0.19	-3.4	0.31	90	Mehmet 1935
30.	<i>M. dissia</i>		"	422	62	139	77	1.21, 0.09	-14.0	0.86	32	Original
31.	<i>Sireblote panda</i> Hbn.		"	2886	59	141	82	0.80, 0.11	22.3	0.50	51	Calvo & Molina 2005
32.	<i>Ennomos subsignarius</i> (Hbn.)		Geometridae	214	41	159	118	1.31, 0.06	-34.7	0.92	36	Drooz 1965
33.	<i>B. piniaria</i>		"	170	60	140	80	1.10, 0.08	-5.2	0.41	313	Gruys 1970
34.	<i>Quadricalcarifera</i>											
	<i>punctatella</i> (Mots.) ^a		Notodontidae	509	29	171	142	1.38, 0.03	-40.1	0.96	77	Kamata & Igarashi 1995
35.	<i>Bombyx mori</i> (L.) ^g		Bombycidae	1275	59	141	82	0.73, 0.08	25.4	0.40	146	Mizuta et al. 1969
Imperfect-uniform												
36.	<i>Tortrix viridana</i> L.		Tortricidae	40	38	162	124	1.05, 0.05	-26.2	0.83	99	Schütte 1957
37.	<i>Archips fuscocupreanus</i> (Wlsm.)		"	62	52	148	96	1.25, 0.07	-20.4	0.81	76	Ohira 1990

continued

TABLE 1. Continued

No.	Species	Family	Pupal weight			Equation ($F_p = bW_p + a$)					Source of data
			Midrange (mg)	Min. (%)	Max. Range (%)	b, SE	a	r ²	n		
38.	<i>Choristoneura fumiferana</i> (Clem.)	NH	78	19	181	162	0.92, 0.11	-23.3	0.61	43	Lorimer & Bauer 1983
39.	"	MN	106	68	132	64	0.60, 0.38	60.7	0.06	45	"
40.	<i>Zeiraphera griseana</i> (Hbn.)	"	28	66	138	72	1.87, 0.29	-105.0	0.52	41	Benz 1974
41.	<i>Cydia pomonella</i> (L.) ^a	"	51	47	153	106	1.19, 0.11	-25.1	0.46	136	Deseö 1971
42.	<i>Parapediasia teterella</i> (Zinck.) ^a	Crambidae	31	51	150	99	1.37, 0.21	-24.2	0.41	66	Marshall 1990
43.	<i>Eoreuma lofini</i> (Dyar)	"	42	36	164	128	0.87, 0.06	8.9	0.83	50	Spurgeon et al. 1995
44.	<i>Agrotis ipsilon</i> (Hufn.)	Noctuidae	259	46	154	108	1.58, 0.02	-58.4	0.98	30	Moawad & Nasr 1978-79
45.	<i>Utetheisa ornatrix</i> (L.)	Arctiidae	137	53	147	94	1.48, 0.13	-59.7	0.53	113	LaMunyon 1997
46.	<i>Pectinophora scutigera</i> (Holdaway)	Gelechiidae	22	73	127	54	0.88, 0.20	2.5	0.42	27	Vickers 1982
47.	<i>Yponomeuta evonymella</i> (L.) ^a	Yponomeutidae	29	48	152	104	0.64, 0.08	34.2	0.79	20	Leather & Mackenzie 1994
48.	<i>Cadra cautella</i> (Wlkr.) ^a	Pyalidae	12	36	176	140	1.17, 0.05	-44.2	0.90	56	Takahashi 1956
Imperfect-multiform											
49.	<i>Spodoptera exigua</i> (Hbn.)	Noctuidae	112	58	142	84	1.29, 0.12	-17.0	0.52	128	Tisdale & Sappington 2001
50.	<i>Diatraea saccharalis</i> (F.) ^f	Crambidae	154	38	162	124	0.99, 0.06	4.6	0.69	116	Bessin & Reagan 1990
51.	<i>Cadra cautella</i> ^a	Pyalidae	28	61	138	77	0.52, 0.18	20.1	0.10	77	Hagstrum & Tomblin 1975
52.	<i>Corcyra cephalonica</i> (Staint.) ^a	"	33	28	171	143	0.80, 0.12	-5.3	0.49	51	Russell et al. 1980
53.	<i>Choristoneura fumiferana</i>	Tortricidae	106	45	137	92	0.97, 0.15	1.24	0.50	42	Original

54. <i>Cnephasia jactatana</i> (Wlkr.)	"	41	76	124	48	1.53, 0.26	-61.1	0.48	41	Ochieng'-Odero 1990
55. <i>Epiphyas postvittana</i> (Wlkr.)	"	30	48	152	104	0.68, 0.18	3.89	0.19	60	Danthanarayana 1975
56. <i>E. postvittana</i> ^a	"	31	21	145	124	0.55, 0.13	35.5	0.19	78	"
57. <i>Lobesia botrana</i> (D. & S.) ^a	"	12	46	154	108	1.45, 0.09	-57.0	0.76	87	Torres-Vila et al. 1999
58. <i>Crociosema plebejana</i> Zell.	"	16	59	141	82	2.09, 0.09	-99.9	0.89	75	Hamilton & Zalucki 1991

^a Pupal wt. estimated as adult wt. x 1.85.

^b Based on numerical data in source.

^c Mont St. Hilaire.

^d Havelock.

^e State or province abbreviation.

^f Pooled data for johnsongrass, corn, and cane var. CP 61-37.

TABLE 2. Regressions relating fecundity, F_p , to pupal weight, W_p , in capital breeders based on transformed values for grouped specimens.

No.	Species	Family	No. groups	Group size	Equation		Source of data
					(F _p = bW _p + a)		
					b	a	
Perfect-uniform							
1.	<i>Antheraea mylitta</i> Drury ^a	Saturniidae	6	20	0.60	34.9	Badhera 1992
2.	<i>Samia cynthia ricini</i> Boisd. ^a	“	6	30	1.98	-96.0	Kotikal et al. 1989
3.	<i>Lymantria dispar</i> (L.) ^a	Lymantriidae	8	1-83	1.40	-47.8	Lozinsky 1961
4.	<i>Dendrolimus spectabilis</i> Butler ^a	Lasiocampidae	14	32-244	1.27	-24.0	Kokubo 1973
5.	<i>D. pini</i> (L.) ^a	“	5	2-19	1.35	-33.6	Rudelt 1935
Perfect-multiform							
6.	<i>Antheraea assama</i> Westw.	Saturniidae	40	10	1.70	-70.5	Barah & Sengupta 1991
7.	<i>Lymantria dispar</i> ^a	Lymantriidae	18	1-58	1.12	-14.4	Lewitt 1934
8.	<i>Dendrolimus punctatus</i> Wlkr., 1 st gen. ^a	Lasiocampidae	40	1-40	1.34	-36.9	Tsai et al. 1958
9.	<i>D. punctatus</i> , wintering gen. ^a	“	65	1-22	1.24	-25.1	“
10.	<i>Hyphantria cunea</i> (Drury)	Arctidae	24	≈30	1.35	-34.5	Morris & Fulton
Imperfect-multiform							
11.	<i>Trichoplusia ni</i> (Hbn.) ^a	Noctuidae	12	10	1.21	-16.2	Henneberry & Kishaba 1966
12.	<i>Diatraea saccharalis</i> (F.) ^a	Crambidae	8	≈29 – ≈90	2.06	-104.1	Van Dinther & Goosens 1970
13.	<i>Hofmannophila</i> <i>pseudospretella</i> (Staint.) ^a	Oecophoridae	21	1-27	1.17	-14.0	Woodroffe 1951

^a Based on numerical data in source.^b Pupal weight estimated as 1.85 x adult weight.

and egg size. Temporally, only one of three pairs of available *Malacosoma disstria* slopes differed significantly—0.58 and 0.72 for Louisiana between 1998 and 1999 ($F = 4.14$; $df = 1, 95$; $P = 0.045$) (transcribed data) (Parry et al. 2001).

Temperature effects. Nine multiform relations involved different larval rearing temperatures among cohort subgroups (Nos. 24, 25, 29–31, 34, 35, 53, and 58 in Table 1), and each relation is discussed below.

Relation 30. This previously unpublished *M. disstria* relation is discussed first because it typifies the effects of multiform rearing temperatures on fecundity-maternal pupal weight relations. The data derive from overwintered egg rings collected in April from quaking aspen, *Populus tremuloides* Michx. (Salicaceae), near International Falls, Minnesota. Larvae hatching from several egg rings were mixed and subdivided into three subgroups. The subgroups were laboratory-reared on source foliage through pupation, one subgroup each at arbitrary temperatures of 20, 25, 30° C in separate growth chambers fluorescent-illuminated on a 12:12 D:N schedule. Rearing containers were transparent, screen-topped 20-liter plastic garment boxes. Foliage was renewed every third day and its turgidity maintained by sealing stem bases in water bottles. Pupae were weighed within 24 hr after transformation and placed singly in 25-ml cream cups for eclosion. A subsample of newly eclosed female adults developing at each temperature was frozen for egg counting. Essentially all *M. disstria* eggs are mature at eclosion (OI = 1).

In the whole sample, mean weights of female pupae reared at 20, 25, and 30° were 326, 461, and 331 mg, and the 461 mg weight at 25° is inferred to be statistically the highest ($F = 65.6$; $df = 2, 109$; $P < 0.001$).

In the subsample, both fecundity and female pupal weight peaked at 25° C (Fig 1a), making their reaction norms across the rearing temperatures congruent. A fecundity-maternal pupal weight relation for each temperature was computed (Fig. 1b), but neither their slopes nor intercepts differed significantly (slope $F = 0.80$; $df = 2, 25$; $P = 0.46$, intercept $F = 0.85$; $df = 2, 25$; $P = 0.44$). The three cohort subgroups are pooled in the summary relation (Fig. 1c, Table 1).

Relation 24. Zwölfer (1933) reared *Lymantria monacha* at six arbitrary constant temperatures from 11–28° C. Both fecundity and female pupal weight peaked at ≈25°, making their reaction norms across the rearing temperatures congruent. Points in the source scatterplot were noncoded, which precluded deconstruction for further analysis.

Relation 25. Maksimovic (1958) reared *Lymantria dispar* at six arbitrary constant temperatures from 15.5–31.9° C. Both fecundity and female pupal weight peaked at ≈15.5°, making their reaction norms congruent. I divided these data into two temperature classes for further analysis, 15.5–24.5° and 27.6–31.9°. Mean female pupal weights were 1533 mg at the cooler temperatures and 1189 at the warmer, and the difference is highly significant (Student's $t = 3.6$; $df = 50$; $P < 0.001$) (tabulated data). Slopes and intercepts of fecundity-maternal weight relations for the two classes were 0.41 and -43.4, and 0.46 and -157.8, neither difference proving significant (slope $F = 0.20$; $df = 1, 48$; $P = 0.66$, intercept $F = 0.72$; $df = 1, 48$; $P = 0.40$) (tabulated data).

Relation 29. Mehmet (1935) reared *Malacosoma neustria* at four arbitrary constant temperatures from 18.5–31.5° C. The mean female pupal weight of 551 mg at 22.7° is inferred to be significantly greater than the

FIG. 1. Fecundity-maternal weight relations in cohorts of *Malacosoma disstria* reared at different constant temperatures. a. Reaction norms of female pupal weight and fecundity to rearing temperatures. Weights based on 21–56 individuals; fecundities based on 4–14 individuals. b. Scatterplot and regressions of fecundity vs. female pupal weight for each rearing temperature. Equations: at 20° C, $F = 0.44W - 19.5$, $r^2 = 0.86$; at 25°, $F = 0.54W - 81.7$, $r^2 = 0.94$; at 30°, $F = 0.56W - 57.3$, $r^2 = 0.90$. c. Scatterplot and summary relation of fecundity vs. female pupal weight after transformation to percentages of pooled midrange values. Equation is $F_p = 1.35W_p - 18.3$, $r^2 = 0.81$.

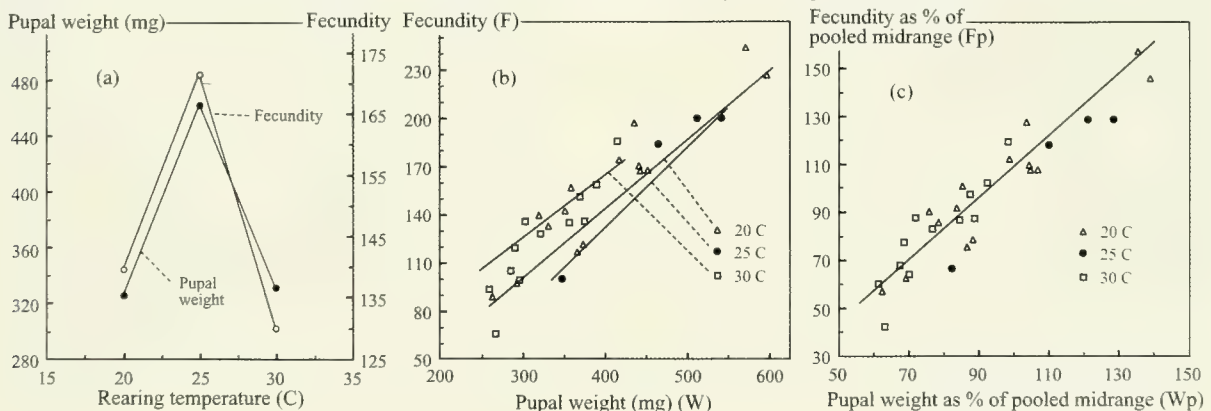
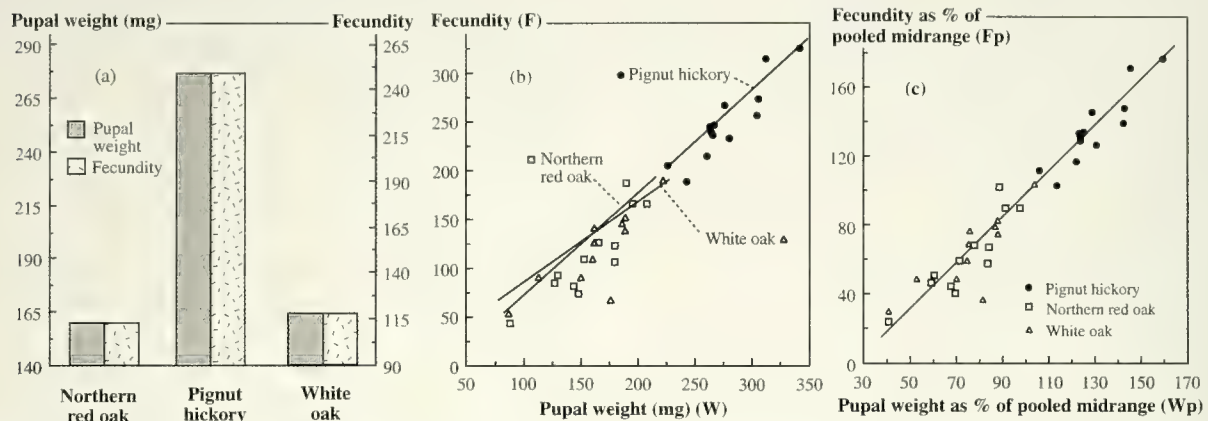


FIG. 2. Fecundity-maternal weight relations in cohorts of *Ennomos subsignarius* reared on different foodplants in the laboratory. a. Pupal weights and fecundities by foodplant. b. Scatterplot of preceding data, with regression statistics as follows: pignut hickory, $F = 1.14 W - 67.1$, $r^2 = 0.81$; northern red oak, $F = 1.11 W - 63.8$, $r^2 = 0.79$; white oak, $F = 0.88 W - 24.9$, $r^2 = 0.66$. c. Scatterplot and summary relation of fecundity vs. pupal weight after transformation to percentages of pooled midrange values. Equation is $F_p = 1.31 W_p - 34.7$, $r^2 = 0.92$. Data transcribed from Drooz (1965).



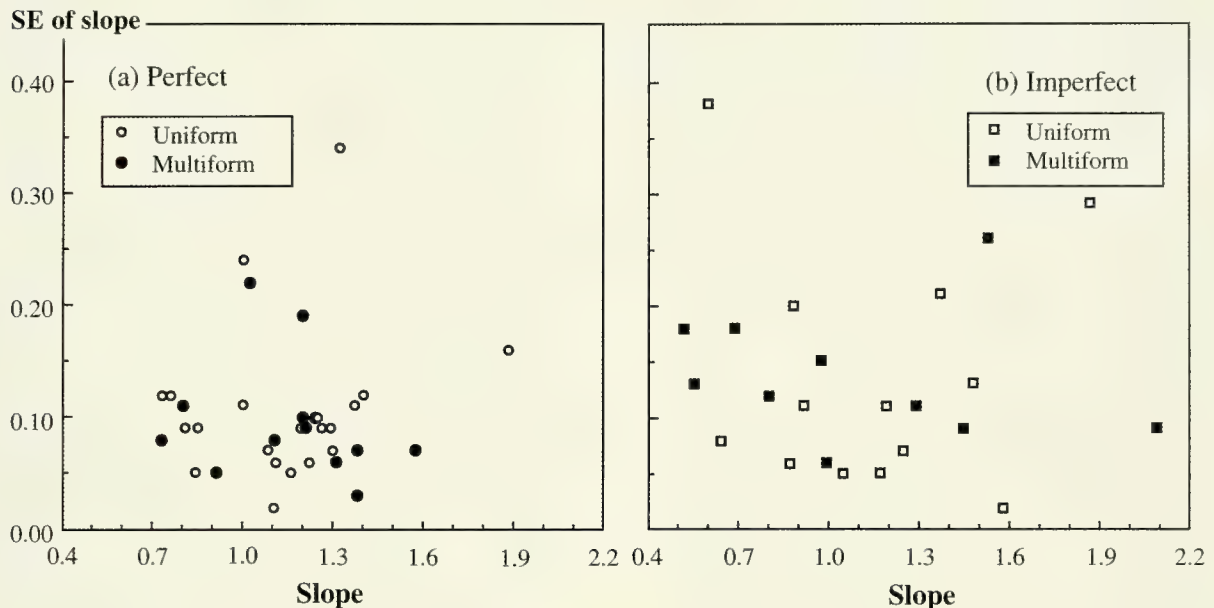
467, 485, and 406 mg at 18.5, 25.4, and 31.5° ($F = 11.55$; $df = 3, 90$; $P < 0.001$) (transcribed data). Both fecundity and female pupal weight peaked at 22.7°, making their reaction norms congruent. Points on the pertinent source scatterplot were not temperature-coded, which precluded deconstruction.

Relation 31. Calvo and Molina (2005) reared *Streblote panda* at four arbitrary constant temperatures from 19–28° C on two foodplants. Congruency of fecundity and maternal weight to the temperatures and foodplants is indeterminate, and the noncoded scatterplot precluded deconstruction.

Relation 34. Kamata and Igarashi (1995) reared *Quadricalcarifera punctatella* at arbitrary constant temperatures from 10–25° C. At the lower temperatures, most larvae had four stadia, and at higher ones, most had five. The authors also field-collected pupae for comparison with the laboratory rearings. Points on their scatterplot of fecundity vs. adult female weight were coded as four-stadium, five-stadium, and field-collected, which permitted deconstruction for analysis and comparison of cohort subgroup regressions. After adult-to-pupal weight conversion, female pupae averaged 390, 520, and 741 mg for the four-stadium (cooler), five-stadium (warmer), and field-collected, all of which are inferred to differ significantly from one another ($F = 391.8$; $df = 2, 74$; $P < 0.001$) (transcribed data). In the three subgroup fecundity-maternal weight relations, slopes and intercepts were 0.72 and -108.4, 0.64 and -74.8, and 0.64 and -48.3. The slopes did not differ significantly ($F = 0.82$; $df = 2, 71$; $P = 0.44$), nor did the intercepts ($F = 0.88$; $df = 2, 71$; $P = 0.42$) (transcribed data). Congruency of fecundity and maternal weight is indeterminate.

Relation 35. Mizuta et al. (1969) reared Japanese and Chinese varieties of *Bombyx mori*, and resulting points on their scatterplot of fecundity vs. female pupal weight were coded as spring or summer and assumed to represent individual specimens. No rearing temperatures were given, but temperatures in spring were likely cooler than those in summer. Mean spring and summer female pupal weights were 1451 and 1133 mg, and the difference, 318 mg, is highly significant (Student's $t = 10.5$; $df = 144$; $P < 0.001$) (transcribed data). Corresponding fecundity-maternal weight slopes and intercepts are 0.30 and 70.8, and 0.45 and -128.3. The slopes do not strictly differ ($F = 3.0$; $df = 1, 142$; $P = 0.085$), nor do the intercepts ($F = 3.79$; $df = 1, 142$; $P = 0.053$). Occurrence of a fecundity-egg size tradeoff could not be ascertained, but given the many varieties of *B. mori* involved here and known generally (Hiratsuka 1999), tradeoffs would not be surprising. Congruency of fecundity and maternal weight is indeterminate.

Relation 53. This previously unpublished *Choristoneura fumiferana* relation is drawn from a two-part experiment. The first part used the whole sample, which focused on the response of female pupal weight to different rearing temperatures. The second part used a subsample of the whole in which fecundity as well as female pupal weight was measured. Certain comparisons in both groups are abbreviated because some data were unfortunately lost as detailed further on. Foliage harboring overwintered second instars within 3 m of the ground was collected in early May from *Abies balsamea* (L.) Mill. and *Picea glauca* (Moench) Voss (both Pinaceae) near Cloquet, Minn. The second instars were light-extracted (Miller 1958) and placed at densities of 1 and 3 per cup in 25 ml

FIG. 3. Funnel diagrams showing standard errors of slopes, SE_b , relative to the corresponding slopes, b . a. Perfect group. b. Imperfect group.

plastic cups with artificial diet. Cups with each density were divided into three subgroups and reared as outlined by Grisdale (1970) in three growth chambers programmed for different temperatures. The first chamber simulated the natural seasonal march of daily mean day-night temperatures based on long-term averages at a weather station ≈ 20 km from the collection site, and presumably approximated the temperature regime to which the insect was acclimated. Chamber temperatures were increased 1°C every 4–6 days during May and June until adult eclosion. At the start, day-night temperatures were 10° and 3° , and at the end, 26° and 12°C . The second and third chambers housed cups at each density, with one chamber programmed 5° cooler than presumed acclimation and the other 5° warmer, their temperatures being increased incrementally as in the first chamber. All chambers were fluorescent-illuminated on a 16:8 D:N schedule. In early June, four weeks after the first collection, fifth instars were collected at the site, placed singly in cups with artificial diet, and added to the experiment for exposure to the rearing temperatures only during the late larval stage, from the latter part of stadium 5 through final stadium 6. All pupae were weighed and sexed within 24 hr after transformation. The subsample for computing fecundity-maternal weight regressions consisted of female-male pupal pairs placed one each with a 6 cm long sprig of foodplant in 0.5 liter cardboard ice cream containers in which they eclosed, mated, and oviposited. The OI of this species is ≈ 0.4 (Outram

1971, Miller 1987), but no liquids were provided to adults during posteclosion ovigenesis. Laid eggs were counted daily, and unladen chorionated eggs were added to the daily counts after females died, with chorionation evaluated by ovarian staining with methylene blue (Miller 1987). As in the whole sample, a subsample subgroup developed under each of three temperature regimes, under long and short exposures to temperature regimes, and at two rearing densities.

In the whole sample, mean weights of long-exposure female pupae at single and triple densities across all temperatures were 100.0 and 101.7 mg, indicating no real difference due to density. Long-exposure single-density female pupal weights at presumed acclimation, at 5° cooler, and at 5° warmer, were 103.8, 106.9, and 85.8 mg, and the 18.0 mg lesser weight at warmer than presumed acclimation is highly significant (Student's $t = 3.75$; $df = 196$; $P < 0.001$). Long-exposure triple-density weights were 99.4, 111.9, and 93.6 mg, and the 12.5 mg greater weight at cooler than presumed acclimation is significant (Student's $t = 2.90$; $df = 248$; $P = 0.006$). Short-exposure single-density female pupal weights were 111.3, 110.8, and 104.7 mg, and the 6.6 mg lesser weight at 5° warmer than presumed acclimation is significant (Student's $t = 2.24$; $df = 293$; $P < 0.038$). The foregoing reliance on t -tests rather than more comprehensive F -tests was necessitated by loss of some data before analysis was completed. In the fecundity-maternal pupal weight subsample with densities and exposure lengths pooled, mean fecundities and mean

female pupal weights at presumed acclimation and 5° warmer were 167.2 and 106.6, and 112.6 and 88.5, indicating congruent reaction norms to rearing temperatures in the surviving data, data from 5° cooler than acclimation having been lost. These subgroup pupal weights mirrored those of the whole sample, but the associated fecundities were depressed compared with published experiments in which females received imbibing liquids (Miller 1987, 1989). Slopes and intercepts of pooled subsample data at presumed acclimation and 5° warmer were 1.26 and 23.2, and 1.91 and -56.3, but although seemingly disparate, neither slopes nor intercepts differed significantly (slope $F = 0.046$; $df = 1, 38$; $P = 0.83$, intercept $F = 0.12$; $df = 1, 38$; $P = 0.75$).

Relation 58. Hamilton and Zalucki (1991) reared *Crociosema plebejana* at a number of arbitrary constant temperatures from 14–31° C. Fecundity and female adult weight were congruent. Their scatterplot of fecundity vs. female adult weight is temperature-coded for seven rearing temperatures, which enabled deconstruction for analysis of constituent regressions. I computed two fecundity-maternal weight regressions, one for 14–21° C, and the other for 25–31°. Their slopes and intercepts were 51.8 and -237.6, and 47.9 and -195.0, and neither the slopes nor intercepts differed significantly (slope $F = 0.64$; $df = 1, 71$; $P = 0.42$, intercept $F = 0.99$; $df = 1, 71$; $P = 0.32$) (transcribed data). In addition, the authors showed statistically that fecundity depended on female weight independently of temperature.

Diet effects. Twelve multiform relations involved cohort subgroups that received different larval diets (Nos. 26, 28, 32, 33, 50, 52, 54–56, 67) or different adult diets (Nos. 49, 51). Subgroup larvae were reared separately on different foodplants or on diets differing otherwise in quality or quantity. In the adult group, different imbibing liquids were provided, or withheld, during posteclosion ovigenesis. Each relation is discussed below.

Relation 32 for *Ennomos subsignarius* is discussed first because it typifies the effect different larval diets have on fecundity-maternal weight relations. Drooz (1965) reared this species on pignut hickory, *Carya glabra* (Mill.) Sweet (Juglandaceae), northern red oak, *Quercus rubra* L., and white oak, *Q. alba* L. (Fagaceae). He found that fecundity and female pupal weight were significantly higher on pignut hickory than on the oaks (transcribed surrogate values here in Fig. 2a). Fecundity and female pupal weight across foodplants were congruent. In a subsample, Drooz computed regressions of fecundity vs. female pupal weight by

individual and pooled foodplants (transcribed surrogate values in Fig. 2b). I confirmed that differences among slopes and intercepts of these regressions do not differ significantly (slope $F = 0.63$; $df = 2, 30$; $P = 0.54$, intercept $F = 0.51$; $df = 2, 30$; $P = 0.50$) (transcribed data). The three subgroups are pooled in the summary relation (Fig. 2c, Table 1).

Relation 26. Cambini and Magnoler (1997) reared cohort subgroups of *Lymantria dispar* on juvenile foliage alone and mixed juvenile-mature foliage of cork oak, *Quercus suber* L., and holm oak, *Q. ilex* L. They showed that female pupae were significantly heavier on cork than on holm oak, and on juvenile than on mixed juvenile-mature foliage. Six-stadium females predominated on cork oak, and 7-stadium females predominated on holm oak. The authors also showed that neither slopes nor intercepts of fecundity-maternal pupal weight relations among the subgroups differed significantly by foodplant. Fecundity and female pupal weight were consistently congruent.

Relation 28. Van der Linde and Voûte (1967) reared *Euproctis chrysorrhoea* on English oak, *Quercus robur* L., and buckthorn, *Rhamnus* sp. (Rhamnaceae), and their scatterplot of fecundity vs. pupal weight was foodplant-coded, which permitted deconstruction. Mean weights of female pupae were 186 mg on English oak and 268 on buckthorn, and the difference, 82 mg, is highly significant (Student's $t = 6.66$; $df = 54$; $P < 0.001$) (transcribed data). Corresponding slopes and intercepts were 1.78 and -112.4, and 1.63 and -62.1, but neither slopes nor intercepts differed significantly (slope $F = 0.31$; $df = 1, 52$; $P = 0.58$, intercept $F = 0.61$; $df = 1, 52$; $P = 0.44$). Congruency of fecundity and female pupal weight is indeterminate.

Relation 33. Gruys (1970) reared *Bupalus piniaria* at different densities including 1 larva/container, considered uncrowded, and 2–5 larvae/container, considered crowded. He presented uncrowded and crowded fecundity-maternal weight scatterplots separately. Mean weights of uncrowded and crowded female pupae were 184 and 152 mg, and the difference, 32 mg, is highly significant (Student's $t = 15.1$; $df = 311$; $P < 0.001$) (transcribed data). Gruys speculated that increased bodily contact in the crowded group adversely affected nutrition. He found that both slopes and intercepts of fecundity-maternal pupal weight regressions differed significantly between the two groups. He also found that crowding significantly reduced mean egg weight, which indicates a fecundity-egg size tradeoff between the two densities. Fecundity and female pupal weight proved congruent. Because density varies naturally, uncrowded and crowded

subgroups are pooled in the summary relation.

Relation 49. Tisdale and Sappington (2001) fed three groups of mated female adult *Spodoptera exigua* different liquid diets—10% honey in water, 10% sucrose in water, and plain water. They showed that fecundity of females on both carbohydrate diets significantly exceeded that of females on plain water. Their diet-specific scatterplots of fecundity vs. female pupal weight allowed deconstruction. I confirmed that pupal weights among treatment groups were statistically equal at the start ($F = 0.51$; $df = 2, 126$; $P = 0.60$) (transcribed data). Slopes and intercepts for the honey, sucrose, and plain water diets were 13.3 and 12.8, 12.4 and 43.6, and 16.5 and 1.78. The slopes did not differ significantly ($F = 1.00$; $df = 2, 122$; $P = 0.37$), nor did the intercepts ($F = 2.03$; $df = 2, 122$; $P = 0.14$) (transcribed data). It should be mentioned that *S. exigua* might be borderline between capital and income breeding.

Relation 50. Bessin and Reagan (1990) field-collected pupae of *Diatraea saccharalis* from two varieties of sugarcane, *Saccharum* spp.; corn, *Zea mays* L.; and johnsongrass, *Sorghum halapense* (L.) Persoon (all Gramineae). They showed that weights of female pupae differed significantly by foodplant but that differences among slopes and intercepts of the corresponding fecundity-size regressions did not differ significantly. Congruency of fecundity and pupal weight is indeterminate.

Relation 51. Hagstrum and Tomblin (1975) provided drinking water to mated female adults of one group of stock-culture *Cadra cautella* and withheld it from a second group. They presented scatterplots of fecundity vs. female weight separately for drinkers and nondrinkers. I confirmed that weights of the two groups were statistically equal at the start (Student's $t = 1.83$; $df = 75$; $P = 0.07$) (transcribed data). The authors found that drinkers laid significantly more eggs than nondrinkers, and that the corresponding fecundity-maternal weight regressions also differed significantly. Drinkers and nondrinkers are pooled in the summary relation because extent of drinking probably varies in environments where this species occurs.

Relation 52. Russell et al. (1980) reared two strains of *Corcyra cephalonica* on grain of millet, *Panicum* sp., and sorghum, *Sorghum* sp. (both Gramineae), which had been adjusted to differing moisture levels from 5–13%. Rearings were separate by strain, foodplant, and level of grain moisture. Mean weight of adult females of both strains ranged from 9.8–21.3 mg between the lowest and highest levels of grain moisture. No statistical tests were reported, but most of the weight differences are probably real. The scatterplot of fecundity vs. adult female weight was not treatment-

coded so could not be deconstructed. Congruency of fecundity and maternal size is indeterminate.

Relation 54. Final instars of *Cnephasia jactatana* were subjected to different levels of starvation to create differences in amount of food ingested (Ochieng'-Odero 1990). The author's scatterplot of fecundity vs. weight of female pupae was not treatment-coded, which precluded deconstruction. Congruency of fecundity and maternal weight is indeterminate.

Relations 55, 56. Dathanararyana (1975) reared *Epiphyas postvittana* on four foodplants—curled dock, *Rumex crispus* L. (Polygonaceae); plantain, *Plantago lanceolata* L. (Plantaginaceae); capeweed, *Arctotheca calendula* L. (Asteraceae); and apple, *Malus sylvestris* (L.) Mill. (Rosaceae). His scatterplots of fecundity vs. female weight were based on separate samples for pupae and adults. Neither scatterplot was diet-coded, which precluded deconstruction, and congruency of fecundity and maternal weight is indeterminate.

Relation 57. Torres-Vila et al. (1999) reared cohort subgroups of *Lobesia botrana* on *Vitis* sp. (Vitaceae), one on inflorescences, a second on unripe fruit, and a third on ripe fruit. These groups simulated three *L. botrana* generations associated with the annual march of foodplant phenology. The authors found that both maternal weight and associated fecundity differed significantly by subgroup. The diet-coded scatterplot allowed deconstruction, and slopes and intercepts for inflorescences, unripe fruit, and ripe fruit were 11.3 and 0.0, 15.5 and -15.5, and 23.8 and -35.1 (transcribed data). The slopes, although seemingly disparate, do not differ significantly ($F = 1.63$; $df = 2, 81$; $P = 0.20$), nor do the intercepts ($F = 0.34$; $df = 2, 81$; $P = 0.71$) (transcribed data). Fecundity and maternal weight proved congruent. The three generations are pooled in the summary relation.

Grouped-specimen relations

The 13 fecundity-maternal pupal weight relations based on grouped specimens number 10 of the perfect kind and 3 of the imperfect, 5 uniform, and 8 multiform. Perfect-uniform and perfect-multiform categories number five each and imperfect-uniform and imperfect-multiform categories number zero and three (Table 2). Grouping damps variation and equally weights groups of differing sample sizes, which biases regression statistics. Presentation of statistics for fecundity-maternal weight relations is therefore limited to slopes and intercepts of summary relations (Table 2) and to cohort subgroup relations, these statistics being useful despite aggregation bias.

Meta-analysis. Slopes of the summary relations vary from 0.60 to 2.06 (Table 2), with mean and SE 1.37 ± 0.10 . This mean is significantly higher than the

1.13 for individual-specimen relations (Student's t [one-tailed test] = 2.30; df = 69; P = 0.04). Slopes of the perfect-uniform category range 0.60–1.98, averaging 1.32; those of the perfect-multiform, 1.12–1.70, averaging 1.35; and those of the imperfect-multiform, 1.17–2.06, averaging 1.48.

Temperature effects. One relation involved different rearing temperatures, as discussed below.

Relation 13. In one experiment, Woodroffe (1951) apparently reared *Hofmannophila pseudospretella* at two temperatures and relative humidities: 25°C–70%, 10°C–70%, and 25°C–20%, but whether larvae were reared or ovipositing adults held under these conditions is not entirely clear. Although Woodroffe reported significant differences in fecundity among some female adult weight classes, I found no differences among adult female weights overall, which averaged 26, 22, and 24 mg (F = 0.31; df = 2, 18; P = 0.74) (tabulated data). I tested differences among the three corresponding fecundity-maternal pupal weight regressions whose slopes and intercepts were 12.8 and -7.4; 10.1 and -0.53; and 10.6 and -24.4, and the slopes did not differ significantly (F = 2.54; df = 2, 15; P = 0.89), nor did the intercepts (F = 0.12; df = 2, 15; P = 0.11) (tabulated data). The three presumed rearings are pooled in the summary relation. In a second rearing experiment mentioned only cursorily, fecundity and female adult weight across three temperature-humidity combinations slightly different than above proved congruent.

Diet effects. Diet was involved in seven relations (Nos. 6–12 in Table 2), each of which is discussed below.

Relation 6. Barah and Sengupta (1991) reared *Antheraea assama* on four foodplants and reported significant differences in female pupal weight by foodplant. Slopes and intercepts of fecundity-maternal pupal weight relations were 84.0 and -334.3 on *Litsaea* sp. No. 1, 47.3 and -95.2 on *Machilus bombycina* King ex Hook, 47.7 and -96.6 on *Litsaea* sp. No. 2, and 33.6 and -23.9 on *Cinnamomum* sp. (all Lauraceae), and the differences were highly significant (slope F = 7.52; df = 3, 32; P < 0.001) (transcribed data). Whether suspected tradeoffs between fecundity and egg size existed by foodplant could not be ascertained. Fecundity and maternal weight were congruent. The foodplants occur together in nature, and data from the four are pooled in the summary relation.

Relation 7. Lewitt (1934) field-collected *Lymantria dispar* pupae from a large area and segregated them into three groups by foodplant damage levels ranging ≈5–100%. Lewitt reported that pupal weight decreased with increasing foodplant damage and attributed this to decreasing food availability. Fecundity and female pupal weight across damage levels were congruent. The data

could not be deconstructed for detailed analysis.

Relations 8 and 9. Tsai et al. (1958) field-collected *Dendrolimus punctatus* pupae of the first and wintering generations from *Pinus* (Pinaceae) and segregated them by three levels of needle damage. Where 50, 80 and 100% of needles were damaged, mean weights of first-generation female pupae were 1210, 940, and 840 mg. Where <50, 50, 80, and 100% of needles were damaged, mean weights of wintering-generation female pupae were 1230, 1680, 1470, and 1490 mg. Although not tested, some differences among the pupal weights of both generations are probably real. Fecundity-maternal weight regressions did not differ among damage levels in either the first generation (slope F = 1.46; df = 2, 34; P = 0.25) or the wintering generation (slope F = 0.03; df = 3, 52; P = 0.99) (tabulated data). However, relations did differ significantly between generations (slope F = 135.2; df = 1, 96; P < 0.001) (tabulated data). Whether suspected tradeoffs between fecundity and egg size occurred could not be ascertained. Fecundity and maternal weight were exactly congruent in the first generation, and approximately so in the wintering generation. A summary relation is tabulated for each generation.

Relation 10. Morris and Fulton (1970) reared *Hyphantria cunea* in different years on different but unspecified diets. Their scatterplot of fecundity vs. female pupal weight was not treatment-coded, which precluded deconstruction for detailed analysis. Congruence of fecundity and maternal weight is indeterminate.

Relation 11. Henneberry and Kishaba (1966) reared 12 groups of *Trichoplusia ni* at 4 densities each with 3 different amounts of artificial diet. Female pupal weights declined significantly with increasing density and decreasing amount of food. Fecundity and maternal weight reaction norms across densities and amounts of food were congruent. The overall relation could not be usefully deconstructed for further analysis.

Relation 12. Van Dinther and Goossens (1970) reared *Diatraea saccharalis* on stalks of rice, *Oryza sativa* L., and corn, *Zea mays* L. (both Gramineae), and on differing amounts of various artificial diets. Magnitudes of reported means, standard deviations, and numbers of test individuals suggest significant differences among female pupal weights. Fecundity and maternal weight were approximately congruent. It was not possible to meaningfully deconstruct the summary fecundity-maternal pupal weight regression for further analysis.

DISCUSSION AND CONCLUSIONS

Exhaustive search yielded 56 more relations, 27 more species, and 8 more families of capital breeders than in

Honek (1993).

Meta-analysis

Few differences in fecundity-maternal pupal weight relations emerged at the metadata level. Individual-specimen slope means for perfect, imperfect, uniform, and multiform categories of summary relations did not differ statistically. The mean slope of 1.37 for the 13 grouped-specimen relations proved significantly higher than the 1.13 for the 58 individual-specimen relations. Also, the mean slope of 1.22 for Honek's (1993) 15 capital breeders exceeded that for the individual-specimen relations, but not significantly. Aggregation bias probably artificially elevated grouped-specimen mean slopes, including Honek's, who divided each data set into 3–8 grouped-specimen values. That the 1.13 slope mean statistically exceeds 1.00 may indicate that fecundity is increased or decreased disproportionately by change in maternal weight. This would indirectly intensify the influence on fecundity by an extrinsic factor like rearing temperature.

Fully deployed meta-analysis seeks to find a single best estimate of an effect or parameter (Gates 2002), but meta-analysis here is not meant to go beyond minimizing bias in selecting data sets and enabling group and subgroup comparisons. Despite evident similarity of slopes among capital breeders, one fecundity-maternal weight relation does not apply to all. Tradeoffs between fecundity and egg size sometimes occur. Also, capital breeders are taxonomically and ecologically diverse, as demonstrated by 15 families represented in this survey. Funnel diagrams of SE_b , plotted on b for imperfect and perfect groups exhibit much scatter, especially in the imperfect group (Fig. 3a, b), which often can indicate low study precision (Gates 2002). However, adult nutrition potential—present in the imperfect group but absent in the perfect—probably increases variation in fecundity, thereby increasing scatter, and adults of the imperfect group usually had access to fluids. Studies of individual imbibing are few, but in one, *Choristoneura fumiferana* females imbibed erratically, which undoubtedly increased variation in fecundity (Miller 1989).

Individual-specimen midrange pupal weights averaging 63 mg for the imperfect group and 1401 mg for the perfect confirm casual observations that perfect capital breeders are typically larger-bodied than imperfect ones.

Extrinsic effects

Extrinsic effects on fecundity-maternal pupal weight relations were reflected predominantly in pupal weight and fecundity. In all nine individual-specimen summary relations involving different rearing temperatures (Nos. 24, 25, 29–31, 34, 35, 53 and 58 in Table 1), female

pupal weight formed steeple-shaped reaction norms across the temperatures, which fecundity closely tracked, as in Fig. 1a. Of the six where cohort subgroups could be compared (Nos. 25, 30, 34, 35, 53, and 58), slopes may have been affected in only one (No. 35 for *Bombyx mori*). Hamilton and Zalucki (1991) showed statistically that in *Crociosema plebejana* (Relation No. 58) fecundity was controlled directly by maternal weight and only indirectly by rearing temperature. In all four individual-specimen summary relations concerning different larval diets where cohort subgroups could be compared (Nos. 26, 32, 33, and 57 in Table 1), female pupal weight and fecundity peaked on the same diet, and only one (No. 33 for *Bupalus piniaria*) exhibited an effect on slope. That maternal weight directly determines fecundity can be inferred from all of the individual-specimen relations.

In the grouped-specimen multiform relations, larval diet was most often the focus, and different diets affected female pupal weight the same as in individual-specimen relations. Although fecundity and maternal weight were congruent in grouped-specimen relations, slopes sometimes differed between cohort subgroups, signaling fecundity-egg size tradeoffs. Different adult diets altered posteclosion ovigenesis in two imperfect capital breeders (Relations 49 and 51 in Table 1), but adult studies were too few to permit broad generalizations.

In a study of maternal weight and fecundity in *Choristoneura fumiferana* developing on normal, fourth- and fifth-year severely infested foliage—a sequence of declining diet quality—Miller (1957) found that the slopes did not differ significantly, but that the intercepts and maternal sizes declined in parallel with the declining diet-quality sequence. In a study whose surprising results need confirmation, Carisey and Bauce (2002) found that maternal size in *C. fumiferana* did not differ among cohort subgroups reared on three artificial diets simulating midcrown, lower crown, and old foliage of *Abies balsamea*, whereas fecundity and egg size declined in parallel with this sequence of declining diet quality.

In several capital-breeder studies not heretofore mentioned, mean fecundity also peaked jointly with mean female pupal weight across rearing temperatures, providing additional examples of congruency. These involved *Galleria mellonella* (L.), *Achroia grisella* (F.) (both Pyralidae), *Bupalus piniaria* (Oldiges 1959), and *Lobesia botrana* (Torres-Vila 1996). Also, in a supplement to Relations 55 and 56 for *Epiphyas postvittana* (Table 1), Danthanarayana et al. (1995) reared *E. postvittana* on four foodplants, including three used in the earlier study, plus an artificial diet, at

six constant temperatures from 10.3–32° C. A 6-temperature \times 5-diet matrix totaling 30 female pupal weights and fecundities resulted. Maternal weight and fecundity peaked exactly together at five of the six temperatures, and did so approximately at the sixth, and exactly together on three of the five diets, and approximately so on the remaining two. The authors showed that most peak fecundities and maternal weights significantly exceeded nonpeak counterparts.

Rearing temperatures in most of the assembled temperature-focused studies were selected arbitrarily, but those for *Choristoneura fumiferana* (Relation 53 in Table 1) were selected purposefully to compare pupal weights and fecundities at warmer and cooler regimes with those at simulated natural temperatures. The natural regime was presumed to represent the regime of acclimation. Pupal weights and fecundities slumped at 5° warmer but peaked at or near 5° cooler. This occurred in both the short- and long-exposure experiments, which suggests that rapidly accelerating weight increase in the late fifth and sixth stadia (Eidt and Cameron 1972) made short exposure virtually equal to long exposure. Thus, brief anomalous warm weather might result in lighter, less fecund females, and brief anomalous cool weather in heavier, more fecund females. More often than not, cooler temperatures produced heavier, more fecund females even though temperatures were selected arbitrarily. Because of its population dynamics interest, this phenomenon should be sought in other capital breeders.

Deconstructing some fecundity-maternal pupal weight relations to obtain cohort subgroup regressions for comparison created smaller samples with fewer degrees of freedom, which may have led to false negatives in some tests of slope differences. Possible examples are *Choristoneura fumiferana*, *Lobesia botrana* (Relations 53 and 57 in Table 1), and *Hofmannophila pseudospretella* (Relation 13 in Table 2). However, these few cases do not seriously challenge the conclusion that extrinsic alteration of slopes occurs infrequently.

Leather (1988) cautioned against interpreting fecundity-size relations simplistically. His point that potential fecundity does not necessarily translate to field fecundity is unarguable. However, Leather's critique envisaged Lepidoptera as a whole without distinguishing between the divergent life systems of capital and income breeders. Also, he did not realize that extrinsic alteration of maternal size does not necessarily alter underlying fecundity-size relations. With the tally of more than 25 exactly congruent maternal pupal weights and fecundities emerging in this survey, and with no clear counter examples, the direct

dependence of fecundity on maternal weight probably warrants the axiomatic status it has been accorded for capital-breeding Lepidoptera. Moreover, extrinsic influences like rearing temperature and larval diet affect the dependence through maternal weight and thus only indirectly.

When slopes differed either spatially or among cohort subgroups, as they did in 10 cases, egg size, where reported, also differed, indicating tradeoffs with fecundity. Spatial examples include *Choristoneura fumiferana* (Harvey 1983) and *Malacosoma disstria* (Parry et al. 2001). A cohort subgroup example is that of *Bupalus piniaria* (Gruys 1970). Although not precisely understood, such tradeoffs are probably adaptive. They raise the possibility not only of their wider occurrence among capital breeders but that reproductive bulk, R —the mathematical product of fecundity \times mean weight of one egg (Roff 1992)—might constitute a reproductive response as useful as fecundity. The expression $R = b(W - R) + a$ removes R from W on the right-hand side of the equation so that maternal weight alone remains. This equation would be suitable where fully independent response and explanatory variables are desirable.

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LITERATURE CITED

- AGWU, W. I. 1974. The population dynamics of *Leucoptera spartiofoliella* (Hb.) (Lepidoptera: Lyonetiidae) in south-eastern England. *J. Anim. Ecol.* 43: 439–453.
- BADHERA, S. 1992. Relationship between pupal dimensions and fecundity in tasar silk worm, *Antheraea mylitta* Drury (Lepidoptera: Saturniidae). *Uttar Pradesh J. Zool.* 12: 37–39.
- BARAH, A. AND A. K. SENGUPTA. 1991. Correlation and regression studies between pupal weight and fecundity of muga silkworm *Antheraea assama* Westwood (Lepidoptera: Saturniidae) on four different foodplants. *Acta Physiol. Hung.* 78: 261–264.
- BENZ, G. 1974. Negative Rückkoppelung durch Raum- und Nahrungskonkurrenz sowie zyklische Veränderung der Nahrungsgrundlage als Regelprinzip in der Populationsdynamik des Grauen Lärchenwicklers, *Zeiraphera diniana* (Guenée) (Lep., Tortricidae). *Z. Angew. Entomol.* 76: 196–228.
- BESSIN, R. T. AND T. E. REAGAN. 1990. Fecundity of sugarcane borer (Lepidoptera: Pyralidae), as affected by larval development on gramineous host plants. *Environ. Entomol.* 19: 635–639.
- BEVAN, D. AND A. PARAMONOV. 1957. Fecundity of *Bupalus piniarius* in Britain, 1955. *Forest. Comm. Rep. For. Res. (Britain)*, 1956, pp. 155–162.
- BOGGS, C. L. 1992. Resource allocation: exploring connections between foraging and life history. *Funct. Ecol.* 6: 508–518.

- BOGGS, C. L. 1997. Reproductive allocation from reserves and income in butterfly species with differing adult diets. *Ecology* 78: 181–191.
- CAIYO, D. AND J. M. MOLINA. 2005. Fecundity-body size relationship and other reproductive aspects of *Streblote panda* (Lepidoptera, Lasiocampidae). *Ann. Entomol. Soc. Amer.* 98: 191–196.
- CAMBINI, A. AND A. MAGNOLIER. 1997. The influence of two evergreen oaks on development characteristics and fecundity of the gypsy moth. *Redia* 80: 33–43.
- CAREY, J. R. 1993. Applied demography for biologists, with special emphasis on insects. 206 pp. Oxford, New York.
- CARISEY, N. AND E. BAUCE. 2002. Does nutrition-related stress carry over to spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae) progeny? *Bull. Entomol. Res.* 92: 101–108.
- DANTHANARAYANA, W. 1975. The bionomics, distribution and host range of the light brown apple moth, *Epiphyas postvittana* (Walk.) (Tortricidae). *Aust. J. Zool.* 23: 419–437.
- DANTHANARAYANA, W., H. GU AND S. ASHLEY. 1995. Population growth potential of *Epiphyas postvittana*, the lightbrown apple moth (Lepidoptera: Tortricidae) in relation to diet, temperature and climate. *Aust. J. Zool.* 43: 381–394.
- DESEÖ, K. V. 1971. Study of factors influencing the fecundity and fertility of codling moth (*Laspeyresia pomonella* L., Lepid., Tortr.). *Acta Phytopath. Acad. Sci. Hung.* 6:243–252.
- DROOZ, A. T. 1965. Some relationships between host, egg potential, and pupal weight of the elm spanworm, *Ennomos subsignarius* (Lepidoptera: Geometridae). *Ann. Entomol. Soc. Amer.* 58: 243–245.
- ECKSTEIN, K. 1911. Beiträge zur Kenntnis des Kiefernspinners *Lasiocampa* (*Gastropacha*, *Dendrolimus*) *pini* L. *Zool. Jahrb. Abt. Syst. Geogr. Biol. Tiere* 31: 59–164.
- EIDT, D. C. AND M. D. CAMERON. 1972. Measuring growth and development in post-diapause spruce budworms (Lepidoptera: Tortricidae). *Can. Entomol.* 104: 1901–1910.
- FISCHER, K. AND K. FIEDLER. 2001. Effects of adult feeding and temperature regime on fecundity and longevity in the butterfly *Lycaena hippothoe* (Lycaenidae). *J. Lepid. Soc.* 54: 91–95.
- FUJIE, A. 1980. Ecological studies on the population of the pear leaf miner, *Bucculatrix pyricorella* Kuroko (Lepidoptera: Lyonetiidae) 3. Fecundity fluctuation from generation to generation within a year. *Appl. Entomol. Zool.* 15: 1–9.
- GATES, S. 2002. Review of methodology of quantitative reviews using meta-analysis in ecology. *J. Anim. Ecol.* 71: 547–557.
- GEERTSEMA, H. 1975. Studies on the biology, ecology and control of the pine tree emperor moth, *Nudaurelia cytherea cytherea* (Fabr.) (Lepidoptera: Saturniidae). *Ann. Univ. Stellenbosch* 50 (A) No. 1, 170 pp.
- GRISDALE, D. 1970. An improved laboratory method for rearing large numbers of spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol.* 102: 1111–1117.
- GRUYS, P. 1970. Growth in *Bupalus piniarius* (Lepidoptera: Geometridae) in relation to larval population density. *Verh. Rijksinst. Natuurbeh.* No. 1, 127 pp.
- HAGSTRUM, D. W. AND C. F. TOMBLIN. 1975. Relationship between water consumption and oviposition by *Cadra cautella* (Lepidoptera: Phycitidae). *J. Georgia Entomol. Soc.* 10:358–363.
- HAMILTON, J. G. AND M. P. ZALUCKI. 1991. Effect of temperature on development rate, survival and fecundity of cotton tipworm, *Crocidosema plebejana* Zeller (Lepidoptera: Tortricidae). *Aust. J. Zool.* 39:191–200.
- HARRISON, S. AND R. KARBAN. 1986. Effects of an early-season folivorous moth on the success of a later-season species, mediated by a change in the quality of the shared host, *Lupinus arboreus* Sims. *Oecologia* (Berlin) 69: 354–359.
- HARVEY, G. T. 1983. A geographical cline in egg weights in *Choristoneura fumiferana* (Lepidoptera: Tortricidae) and its significance in population dynamics. *Can. Entomol.* 115: 1103–1108.
- HAUKIOJA, E. AND S. NEUVONEN. 1985. The relationship between size and reproductive potential in male and female *Epirrita autumnata* (Lep., Geometridae). *Ecol. Entomol.* 10: 267–270.
- HENNEBERRY, T. J. AND A. N. KISHABA. 1966. Pupal size and mortality, longevity, and reproduction of cabbage loopers reared at several densities. *J. Econ. Entomol.* 59: 1490–1493.
- HIRATSUKA, E. 1999. Silkworm breeding. Balkem, Rotterdam. 500 pp. Translation of *Nihon Sanhinsyu Jitsuyokeifu*, Tokyo, 1969.
- HOLLIDAY, N. J. 1977. Population ecology of winter moth (*Operophtera brumata*) on apple in relation to larval dispersal and time of bud burst. *J. Appl. Ecol.* 14: 803–813.
- HONEK, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos* 66:483–492.
- HUEY, R. B. AND D. BERRIGAN. 2001. Temperature, demography, and ectotherm fitness. *Amer. Nat.* 158: 204–210.
- IGBINOSA, I. B. 1992. Field and laboratory techniques for assessing infestations of the nettle caterpillar, *Latona viridissima* Holland (Lepidoptera: Limacodidae). *Ins. Sci. Appl.* 13: 389–398.
- JERVIS, M. A. AND P. N. FERNS. 2004. The timing of egg maturation in insects: ovigeny index and initial egg load as measures of fitness and of resource allocation. *Oikos* 107: 449–460.
- KAMATA, N. AND M. IGARASHI. 1995. Relationship between temperature, number of instars, larval growth, body size, and adult fecundity of *Quadralcarifera punctatella* (Lepidoptera: Notodontidae): cost-benefit relationship. *Environ. Entomol.* 24: 648–656.
- KIKUZAWA, K., T. ASAI AND Y. HIGASHURA. 1979. Leaf production and the effect of defoliation by the larval population of the winter moth, *Operophtera brumata* L. in an alder (*Alnus inokumae* Muir et Kusaka) stand. *Jap. J. Ecol.* 29: 111–120.
- KLOMP, H. 1966. The dynamics of a field population of the pine looper, *Bupalus piniarius* L. *Adv. Ecol. Res.* 3: 207–305.
- KOKUBO, A. 1973. The variations in pupal weight and number of ovarian eggs of the pine moth, *Dendrolimus spectabilis* Butler. *J. Jap. For. Soc.* 55: 283–285. [Japanese]
- KOTIKAL, Y. K., D. N. R. REDDY, A. S. PRABHU, G. G. BHAT AND S. PUSHPALATHA. 1989. Relationship between pupal size and egg production in eri silkworm *Samia cynthia ricini* (Lepidoptera: Saturniidae). *Indian J. Seric.* 28: 30–32.
- KRISTENSEN, N. P. AND A. W. SKALSKI. 1999. Phylogeny and palaeontology, pp. 7–25. In Kristensen, N. P. [Ed.], *Lepidoptera, moths and butterflies*. Vol. 1, Evolution, systematics, and biogeography. De Gruiter, New York.
- LAMUNYON, C. W. 1997. Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. *Ecol. Entomol.* 22: 69–73.
- LEATHER, S. R. 1988. Size, reproductive potential and fecundity in insects: things aren't as simple as they seem. *Oikos* 51:386–388.
- LEATHER, S. R. AND G. A. MACKENZIE. 1994. Factors affecting the population development of the bird cherry ermine moth, *Yponomeuta evonymella* (L.). *Entomologist* 113: 86–105.
- LEWITT, M. M. 1934. Variability of pupae and of the fecundity of butterflies of the gypsy moth (*Porthetria dispar* L.). *Trav. Inst. Zool. Biol. Acad. Sci. D'Ukraine.* 2: 135–170. [Ukrainian, English summary]
- LORIMER, N. 1979. Patterns of variation in some quantitative characters of *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *Ann. Entomol. Soc. Amer.* 72: 275–280.
- LORIMER, N. AND L. S. BAUER. 1983. Spruce budworm weight and fecundity: means, frequency distributions, and correlations for two populations (Lepidoptera: Tortricidae). *Great Lakes Entomol.* 16: 153–156.
- LOZINSKY, V. A. 1961. On the correlation existing between the weight of pupae and the number and weight of eggs of *Lymantria dispar* L. *Zool. Zhur.* 40: 1571–1573. [Russian, English summary]
- MADRID, F. J. AND R. K. STEWART. 1981. The influence of some environmental factors on the development and behavior of the gypsy moth (*Lymantria dispar* L.) in Quebec. *Ann. Soc. Entomol. Québec* 26: 191–211.
- MAKSIMOVIC, M. 1958. Experimental research on the influence of temperature upon the development and the population dynamics of the gypsy moth (*Liparis dispar* L.). Translation published by NOLIT Publ. House, Belgrade, Yugoslavia, OTS 61–11203, 95 pp.

- MARSHALL, L. D. 1990. Intraspecific variation in reproductive effort by female *Parapediasia teterrella* (Lepidoptera: Pyralidae) and its relation to body size. *Can. J. Zool.* 68: 44–48.
- MEHMET, B. 1935. Experimentelle Untersuchungen über den Einfluss von Temperatur und Luftfeuchtigkeit auf die Sterblichkeit und Entwicklung des Ringelspinner, *Malacosoma neustria* L. *Z. Angew. Entomol.* 21: 501–522.
- MILLER, C. A. 1957. A technique for estimating the fecundity of natural populations of the spruce budworm. *Can. J. Zool.* 35: 1–13.
- MILLER, C. A. 1958. The measurement of spruce budworm populations and mortality during the first and second larval instars. *Can. J. Zool.* 36: 409–422.
- MILLER, T. A., W. J. COOPER AND J. W. HIGHFILL. 1982. Relationships between pupal size and egg production in reared female *Antheraea polyphemus*. *Ann. Entomol. Soc. Amer.* 75: 107–108.
- MILLER, T. A., W. J. COOPER AND J. W. HIGHFILL. 1983. Egg production in female *Callosamia promethea* (Lepidoptera: Saturniidae) as a function of pupal size and adult longevity. *Ann. Entomol. Soc. Amer.* 76: 668–670.
- MILLER, W. E. 1987. Spruce budworm (Lepidoptera: Tortricidae): role of adult imbibing in reproduction. *Environ. Entomol.* 16: 1291–1295.
- MILLER, W. E. 1989. Reproductive enhancement by adult feeding: effects of honeydew in imbibed water on spruce budworm. *J. Lepid. Soc.* 43: 167–177.
- MILLER, W. E. 1996. Population behavior and adult feeding capability in Lepidoptera. *Environ. Entomol.* 25: 213–226.
- MIZUTA, Y., T. HONOUÉ AND T. WADA. 1969. Relationship between weight of pupae and number of eggs by moths of the silkworm, *Bombyx mori*. *Bull. Sericult. Exp. Stn. (Japan)* 23: 515–532.
- MOAWAD, G. M. AND E.-S. A. NASR. 1978–79. The correlation between pupal weight and pupal duration, moth longevity and number and weight of eggs of the greasy cutworm, *Agrotis ipsilon* (Hufn.). *Bull. Soc. Entomol. Egypte* 62: 257–261.
- MORRIS, R. F. AND W. C. FULTON. 1970. Models for the development and survival of *Hyphantria cunea* in relation to temperature and humidity. *Mem. Entomol. Soc. Can.* 70, 60 pp.
- OCHIENG'-ODERO, J. P. R. 1990. Critical, pupal and adult weights in the size related metamorphosis of the black lyre leafroller '*Cnepharia jactatana*'. *Entomol. Exp. Appl.* 54: 21–27.
- OHIRA, Y. 1990. Reproductive biology of the apple tortrix, *Archips fuscocupreanus* Walsingham (Lepidoptera: Tortricidae). *Bull. Fruit Tree Res. Sta.* 17: 63–76. [Japanese, English summary]
- OLDIGES, H. 1959. Der Einfluss der Temperatur auf Stoffwechsel und Eiproduktion von Lepidopteren. *Z. Angew. Entomol.* 44: 115–166.
- OUTRAM, I. 1971. Morphology and histology of the reproductive system of the female spruce budworm, *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. Entomol.* 103: 32–43.
- PARRY, D., R. A. GOYER, AND G. J. LENHARD. 2001. Macrogeographic clines in fecundity, reproductive allocation, and offspring size of the forest tent caterpillar *Malacosoma disstria*. *Ecol. Entomol.* 26: 281–291.
- ROFF, D. A. 1992. The evolution of life histories. 535 pp. Chapman & Hall, New York.
- ROSSITER, M. C. 1991. Maternal effects generate variation in life history: consequences of egg weight plasticity in the gypsy moth. *Funct. Ecol.* 5: 386–393.
- RUDELT, J. 1935. Über die Beziehungen zwischen Puppengewicht und Eiproduktion beim Kiefernspinner (*Dendrolimus pini* L.). *Anz. Schädlingk.* 11: 1–6.
- RUSSELL, V. M., G. G. M. SCHULTEN AND F. A. ROORDA. 1980. Laboratory observations on the development of the rice moth *Corcyra cephalonica* (Stainton) (Lepidoptera: Galleriinae) on millet and sorghum at 28° and different relative humidities. *Z. Angew. Entomol.* 89: 488–498.
- SCHÜTTE, F. 1957. Untersuchungen über die Populationsdynamik des Eichenwicklers (*Tortrix viridana* L.). *Z. Angew. Entomol.* 40: 1–36, 285–331.
- SHIGA, M. 1977. Population dynamics of *Malacosoma neustria tacea* (Lepidoptera: Lasiocampidae): stabilizing process in a field population. *Res. Popul. Ecol.* 18: 284–301.
- SINGH, Y. R. AND B. PRASAD. 1987. Correlation among body weight, pupal weight and fecundity of eri silkworm, *Philosamia ricini* Hutt. (Lep.: Saturniidae). *Sericologia* 27: 49–60.
- SPITZER, K., M. REJMANEK AND T. SOLDÁN. 1984. The fecundity and long-term variability in abundance of noctuid moths (Lepidoptera, Noctuidae). *Oecologia (Berlin)* 62: 91–93.
- SPURGEON, D. W., P. D. LINDGREN, T. N. SHAVER AND J. R. RAULSTON. 1995. Realized and potential fecundity of the Mexican rice borer (Lepidoptera: Pyralidae) as a function of pupal weight. *Environ. Entomol.* 24: 94–98.
- STAHL, G. 1939. Ueber die Beziehungen zwischen Puppendurchmesser, Puppengewicht, Puppenvolumen und Eizahl beim Kiefernspinner, *Bupalus piniarius*. *Forstarchiv* 10: 113–126.
- SYSTAT: statistics, version 5.2 ed. 1992. SYSTAT Inc., Evanston, Illinois.
- TAKAHASHI, F. 1956. On the effect of population density on the power of reproduction of the almond moth, *Ephesia cautella*. 1. On the relationships between the body size of the moth and its fecundity and longevity. *Jap. J. Appl. Zool.* 21: 78–82. [Japanese, English summary]
- TAMMARU, T. AND E. HAUKIOJA. 1996. Capital breeders and income breeders among Lepidoptera—consequences to population dynamics. *Oikos* 77: 561–564.
- TISDALE, R. A. AND T. W. SAPPINGTON. 2001. Realized and potential fecundity, egg fertility, and longevity of laboratory-reared female beet armyworm (Lepidoptera: Noctuidae) under different adult diet regimes. *Ann. Entomol. Soc. Amer.* 94: 415–419.
- TITSCHACK, E. 1922. Beiträge zu einer Monographie der Kleidermotte, *Tineola biselliella*. *Z. Techn. Biol.* 10: 1–168.
- TORRES-VILA, L. M. 1996. Efecto de la temperatura de desarrollo preimaginal sobre el potencial biótico de la polilla del racimo de la vid, *Lobesia botrana* (Denis y Schiffermüller, [1775]) (Lepidoptera: Tortricidae). *SHILAP Revta. Lepid.* 24: 197–206.
- TORRES-VILA, L. M., M. C. RODRIGUEZ-MOLINA, R. ROHRICH AND J. STOCKEL. 1999. Vine phenological stage during larval feeding affects male and female reproductive output of *Lobesia botrana* (Lepidoptera: Tortricidae). *Bull. Entomol. Res.* 89: 549–556.
- TSAI, P.-H., Y.-C. LIU, T.-C. HOW, C.-Y. LI AND C. HO. 1958. Preliminary study on the development of the pine caterpillar, *Dendrolimus punctatus* Walker, under different conditions of injury of the host plant. *Acta Entomol. Sinica* 8: 327–334. [Chinese, English summary]
- VAN DER LINDE, R. J. AND A. D. VOÛTE. 1967. Das Auftreten des Goldafters (*Euproctis chrysorrhoea* L.) in den Niederlanden und der mögliche Einfluss der Nahrung auf die Schwankungen in der Populationsdichte. *Z. Angew. Entomol.* 60: 85–96.
- VAN DINTHER, J. B. M. AND P. A. GOOSSENS. 1970. Rearing of *Diatraea saccharalis* on diets in Surinam. *Entomol. Exp. Appl.* 13: 320–326.
- VICKERS, R. A. 1982. Some aspects of reproduction in *Pectinophora scutigera* (Holdaway) (Lepidoptera: Gelechiidae). *J. Aust. Entomol. Soc.* 21: 63–68.
- WOODROFFE, G. E. 1951. A life history study of the brown house moth, *Hofmannophila pseudospretella* (Staint.) (Lep., Oecophoridae). *Bull. Entomol. Res.* 41: 529–553.
- YADAV, G. S. AND B. C. GOSWAMI. 1999. Correlation and regression studies between different quantitative characters of muga silkworm *Antheraea assamensis* Helfer during two commercial crops. *Bull. Indian Acad. Sericult.* 3: 12–20.
- YADAV, G. S., B. M. K. SINGH, B. R. R. P. SINHA AND K. THANGAVELU. 2001. Studies on association between moth weight and potential fecundity of ecorace Bhandara of tasar silk moth (*Antheraea paphia* Linn.). *Bull. Indian Acad. Sericult.* 5: 59–67.
- ZWÖLFER, W. 1933. Studien zur Ökologie, insbesondere zur Bevölkerungslehre der Nonne, *Lymantria monacha* L. *Z. Angew. Entomol.* 20: 1–50.

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PHENOLOGICAL “RACES” OF THE *HESPERIA COLORADO* COMPLEX (HESPERIIDAE) ON THE WEST SLOPE OF THE CALIFORNIA SIERRA NEVADA

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ABSTRACT. On the west slope of the California Sierra Nevada, the subspecies *Hesperia colorado harpalus* (formerly generally known as *H. comma yosemite*) is univoltine, flying in midsummer at mid-elevations. In a number of sites, mostly on serpentine and other unusual soils, a variable but usually slightly darker *colorado* entity flies at similar elevations in September and October. The two are indistinguishable by male genitalia and thus far by mitochondrial DNA sequences. The autumn “race” is usually parapatric with the summer one and is sympatric with it at one known site. The hypothesis that the autumn “race” represents Sierran populations of subspecies *tildenii* of the North Coast Range is not consistent with our DNA data. Due to complete temporal isolation, the two “races” of *H. comma* are functioning as effective biological species.

Additional key words: serpentine, allochronic isolation, speciation, phylogeography, mitochondrial DNA.

Among the many mechanisms suggested for sympatric speciation, temporal (allochronic) isolation has been posited frequently, but rarely supported on further inquiry (Alexander and Bigelow 1960, Harrison and Bogdanowicz 1995, Huang et al. 2000 but see Feder et al. 1994). Allochronic isolation between close relatives is itself common enough, however, whether or not it is a cause of speciation (Coyne and Orr 2004). Two of the most compelling cases for allochronic speciation - sympatric or not - occur in North American Lycaenid butterflies of the genera *Apodemia* (Pratt and Ballmer 1991) and *Euphilotes* (Pratt 1994, Pratt and Emmel 1998). In both genera, allochronic “races” or “biotypes” have arisen within morphospecies, reflecting adaptation to specific hosts in the large Polygonaceous genus *Eriogonum*. The feeding biology of these insects requires close tracking of host flowering phenology, which varies widely among species. The “races” are frequently sympatric, even over wide areas, but since they are completely isolated they are functioning as effective species. They may have diverged too recently to show significant differentiation at the molecular level (Peterson 1995). Allochrony is also a factor in incipient speciation by “host races” in the Cupressaceous-feeding Lycaenid genus *Mitoura* (Nice and Shapiro 2001). In this case also, butterfly phenology is most likely a function of host phenology (i.e. the availability of new growth), as host association is a better predictor than altitude of adult flight period in areas where races overlap geographically (though the relationship between host phenology and the preference and performance of butterflies is complex, see Forister

2005). We here report a case of sympatric, allochronic “races” in the *Hesperia colorado* (Scudder) complex (Hesperiidae) in the Sierra Nevada of California, with no obvious adaptive relation to host phenology.

ECOGEOGRAPHY OF THE “RACES”

These skippers belong to a circumpolar (Holarctic) complex historically called collectively *Hesperia comma* (L.). Recent authors have split off the Nearctic members of this complex, except those of the far Northwest, as a separate species, *H. colorado* (Scudder). The complex was studied phylogeographically by Forister, Fordyce and Shapiro (2004), whose findings broadly support this division. Within the Nearctic range (excluding the far Northwest), these authors found the maximum geographic structure for the mitochondrial gene (COII) they studied to be in California, with two major genetic discontinuities centered around the Sierra Nevada and Transverse Ranges.

The subspecific nomenclature of the populations at issue is very confused. Historically, east-slope Sierra Nevada populations were placed in subspecies *harpalus* (W.H. Edwards) and west-slope ones, which are phenotypically quite different, in subspecies *yosemite* Leussler. Scott (1998) found that the conventional usages were incorrect and that these two names are in fact synonyms and *harpalus* is the correct name for the west-slope entity, while the correct name of the east-slope one is *H. c. idaho* (W.H. Edwards). We review this taxonomy because in using the subspecies as redefined by Scott in this paper, we risk causing confusion in the context of virtually all prior

publications on the group. The name applied to the Inner North Coast Range subspecies (*tildeni* H.A. Freeman) is unaffected.

Both west-slope *harpalus* and east-slope *idaho* are univoltine (as is the entire complex) and fly in early-to-midsummer. Coast Range *tildeni* fly later, typically from August through October. In the early 1970s one of us (AMS) discovered a population near 1500m in Nevada County, CA on the Sierran west slope that flew only in September and October. AMS continued to monitor this population annually. In 1988 it was included in a permanent monitoring site on his altitudinal transect across California and has thus been visited approximately biweekly except in winter since then. Its autumnal flight period has remained constant throughout. It is limited to a serpentine barren with sparse vegetation, much bare rock and only one nectar source, a distinctive dwarfed ecotype of rabbitbrush, *Chrysothamnus nauseosus* (Pallas) Britton (Asteraceae), during its flight season.

Populations of summer-flying *H. c. harpalus* occur in the same canyon at 850m and 1525m on metasedimentary substrates (phyllite and complex schists) at distances of 4 and 11 km respectively, as well as at 2100m on an andesitic mudflow and granodiorite, 40.5 km away. The phenology of these three

populations (identified as Washington, Lang Crossing, and Donner Pass) is compared with the autumnal one (identified as Washington Serpentine) in Figs. 1 and 2. The serpentine population (Washington serpentine) is later-flying than the 850m Washington population

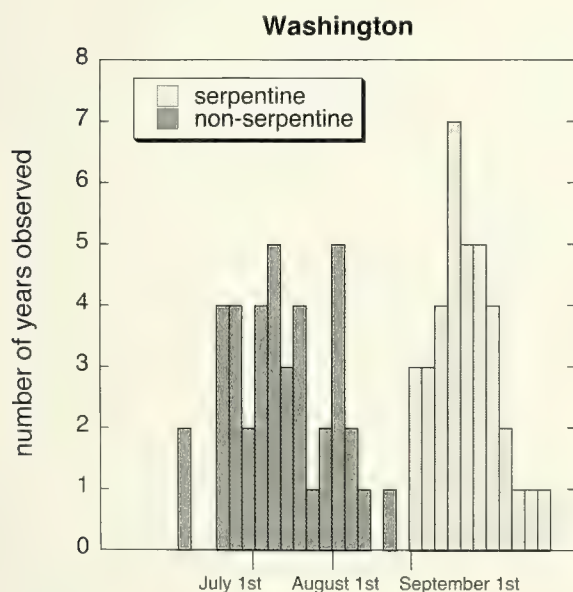


FIG. 1. Histogram showing the phenology of the two *H. colorado* races at Washington (Nevada Co.) since 1988. Vertical bars correspond to five day increments (the beginning of July, August, and September are shown for reference). For example, there were five years in which non-serpentine *H. colorado* individuals were observed at this site during the first five days of August.

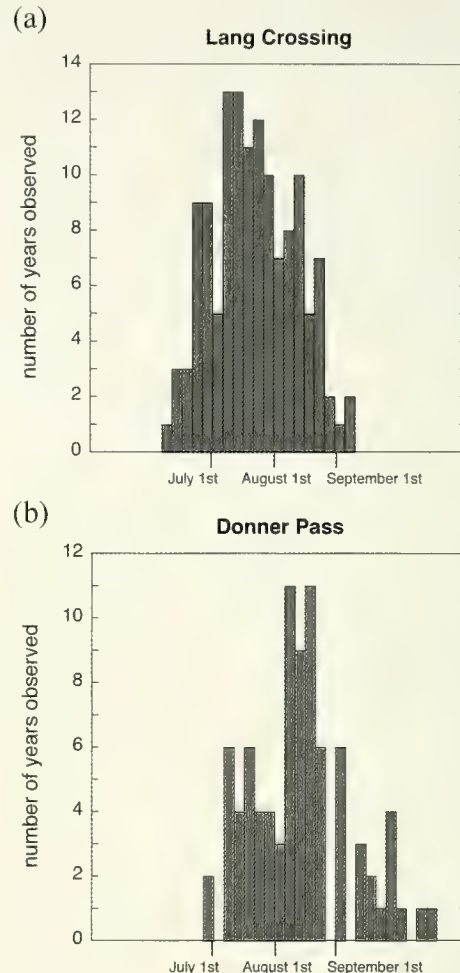


FIG. 2. (a) Histogram showing the number of times that *H. colorado* individuals have been observed throughout the year at Lang Crossing (Nevada Co.) since 1974, and (b) at Donner Pass (Nevada Co.) since 1973. As in Fig. 1, time on the x-axis is expressed in vertical bars indicating observations made within five day intervals.

(there is no overlap), and only overlaps with the 1525m Lang Crossing population by a few days. Individuals at the 2100m Donner Pass population have been observed as late into the fall as at the serpentine population, but this is clearly a phenological effect of high-elevation conditions (there is only one brood at Donner Pass).

Once alerted to the presence of an autumnal race on unusual soils, AMS and his associates began looking for additional autumn-flying populations, primarily on serpentine. Gervais and Shapiro (1999) reviewed the

distributions of edaphic-endemic butterflies in the Sierra Nevada, including the autumn "race" of *H. colorado* (there called *comma*). They reported populations on serpentine and gabbro soils in Nevada, Placer and El Dorado Counties on the west slope, as well as one on limestone in Calaveras County and one on an undetermined substrate in Mariposa County (reported to us by Oakley Shields). There are undoubtedly more populations to be found, and the association with unusual soils may be more apparent than real since we mainly looked for them on such substrates. The populations we identified all appear to be parapatric with summer *harpalus* on "normal" substrates nearby, except one (Drum Powerhouse Road, Placer County, in the Bear River drainage) in which

they are actually sympatric, but allochronic, in an area where serpentine and metasedimentary rocks are intimately interdigitated, and some of the serpentine is unusually mesic.

We have been unable to find any male genitalic differences between these "races" (C.D. MacNeill, pers. comm.). The phenotypes of the autumn "race" are about as variable as summer *harpalus*, though on average slightly darker with a more defined ventral hind wing pattern. Fig. 3 illustrates the phenotypes. We have not identified any consistent character in either sex which can be used to identify flight date correctly. (It should be noted that some individuals of the autumn "race" rather closely resemble the apparent hybrid swarm between east- and west-slope subspecies in the

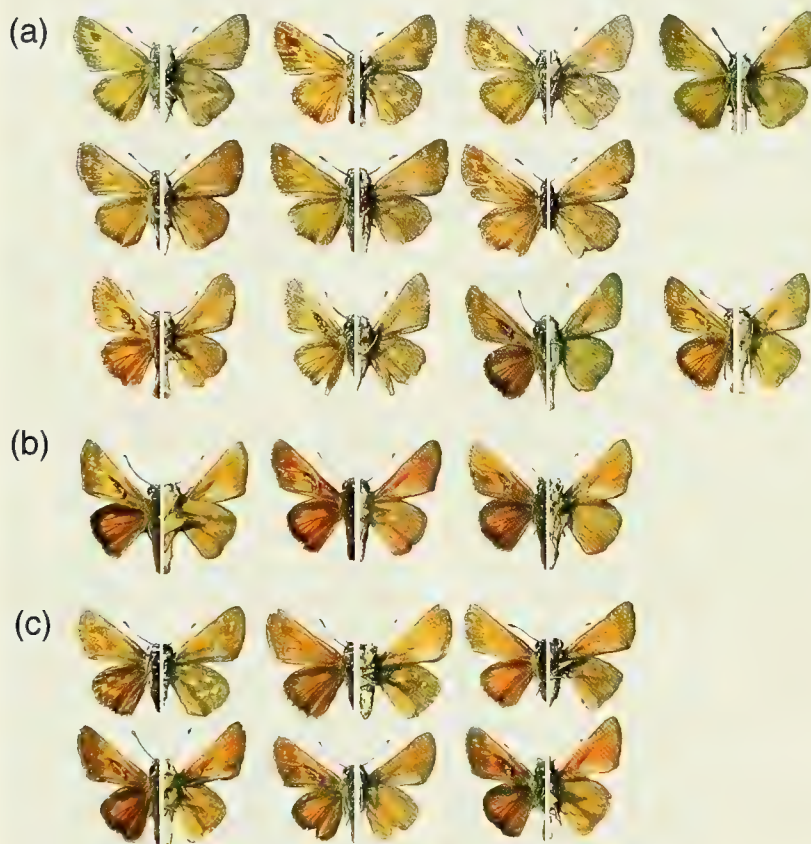


FIG. 3. Photographs of *H. colorado* specimens (showing left dorsal and ventral views): (a) seven females and four males, serpentine "race" from Washington, (b) three males, non-serpentine "race" from Washington, (c) three males and three females, from Lang Crossing.

Feather River Canyon farther north in the Sierra. These animals fly very early, in May and June.) Molecular-genetic evidence bearing on the identity of the autumn "races" is discussed below.

DISCUSSION

An endemic late-season serpentine subspecies of *Hesperia colorado*, described from the Siskiyou mountains of far northern California, was named *mattoonorum* by McGuire (1998). This entity is darker on average than nearby non-serpentine populations, but is also variable. Those nearby populations are extremely variable and confusing. Scott (1998) synonymized the usual name applied to them, *oregonia* (W.H. Edwards), with *harpalus* as well. In our judgment his fixation of the type locality of *oregonia* as "Sierra Nevada Mts., west of Carson City," is unjustified by the historical and biological facts. In any case, Shapiro, Palm and Weislo (1981) recorded *tildeni*-type foothill *H. colorado* in the Trinity Alps from 7-29 August; "light" *oregonia* (from rain-shadow areas) from 16 August - 20 September, and "dark" *oregonia* (from wetter areas) from 12 July through 25 September. The very long type series of *mattoonorum* was collected in September. Shapiro (1991) illustrated a hypervariable population series from a serpentine site in the nearby Trinity Divide, collected 5 September. Because of the very extended flight seasons of far northern California *colorado*, it is difficult to assess the significance of the late flight season of *mattoonorum*. No *mattoonorum* were available for molecular-genetic study, but several specimens from the upper foothills of the Trinity Alps above French Gulch were used.

When Gervais and Shapiro (1999) discussed the geography of edaphic-endemic Sierran butterflies, they proposed the hypothesis that the autumn "races" of *H. colorado* were actually populations of the late-season-flying Inner Coast Range subspecies *tildeni*, signifying a double invasion of the Sierra. This was suggested by the fact that most of the edaphic-endemic entities they found were much more widespread in the Coast Range (and had been largely or entirely overlooked in the Sierra) and that their ranges in the Sierra, including autumn *colorado*, were largely concordant, suggesting a common history.

Forister, Fordyce and Shapiro (2004) found for a portion of the COII mitochondrial gene, coast Range *tildeni* possessed a unique haplotype (D) not found in far-northern California and Oregon or in the Sierra Nevada (see Fig. 1 in Forister *et al.* (2004) for the distribution of haplotypes in the Western United States). The Sierran east and west slopes shared no haplotypes, except in the thoroughly mixed Feather

River hybrid population. They sequenced COII from 5 Washington serpentine animals (Nevada County), all of which were haplotype A, the most common haplotype on the Sierran west slope and in Oregon. Haplotype A does not occur in Coast Range *tildeni*, and is two mutational steps removed from the *tildeni* haplotype D in the statistical parsimony network described by Forister *et al.* (2004). Three Lang Crossing *harpalus* were A, two B; one summer *harpalus* from Drum Powerhouse Road was A (B is one mutational step from A). The serpentine series seems unusually invariant, but cannot be distinguished from nearby summer *harpalus*. On the other hand, the hypothesis that it is really *tildeni* is not supported by our data since haplotype D was not found. Two individuals from the foothills of the Trinity Alps were haplotype B, one I (B is connected to I by one mutational event, and I is two steps removed from A).

Forister *et al.* (2004) found no geographically patterned variation for the nuclear gene *wingless* in North America south of British Columbia. We are thus unable at this time to identify any genetic discontinuity between summer *harpalus* and the autumn "race" in the Sierra Nevada. It is possible that a survey of nuclear variation encompassing a larger portion of the genome would reveal such differences, but we have been unwilling to sample these mostly very small populations to the extent needed for statistical rigor.

Unlike the *Eriogonum*-feeding Lycaenids with phenological "races," there is no obvious connection between the seasonality of these *Hesperia* and their presumed host plants, perennial bunchgrasses. We do not know the hosts used by them at any of the sites mentioned except Lang Crossing, where summer *harpalus* routinely uses the naturalized European grass *Anthoxanthum odoratum* L. (Poaceae). This grass does not occur at any of our other sites in the region. *Hesperia colorado* overwinters as an egg, and larvae feed on young growth in the spring. The flight season of the adults thus appears decoupled from any need to match host phenology, although it could be related to the ability of the eggs to tolerate late-summer desiccation prior to the onset of winter. Until appropriate experiments are done, we will be unable to state whether the autumn "races" are genetically programmed to emerge at that season or are somehow induced physiologically to do so as a result of the nutritional properties of their hosts — which in turn could be affected by occurrence on serpentine vs. non-serpentine substrates. We do not know if the northern entity *mattoonorum* is in any way connected with the Sierran serpentine populations, or whether autumn "races" in the Sierra are all derived from a single

ancestor or have arisen repeatedly in various locations from local summer *harpalus*, in the manner of many plant ecotypes which are generated over and over again. Our nearest sample to *mattoonorum*, from French Gulch (Trinity County), is not that entity and is thus not informative.

CONCLUSIONS

1. Local autumn-flying "races" of *Hesperia colorado* occur within the range of summer-flying subspecies *harpalus* on the west slope of the Sierra Nevada. Most of these known to date are on serpentine or other unusual soils.

2. These autumn "races" average a little darker than nearby *harpalus* but have no definitive wing, genitalic, or molecular characters to allow them to be identified without collection dates.

3. Despite similar seasonality and biogeographic arguments, molecular phylogeography has not supported the hypothesis that the Sierran autumn "races" are actually the Inner Coast Range subspecies *tildeni*.

4. Further study is needed to distinguish between genetic and environmental/physiological factors as determinants of the aberrant phenology of these "races."

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LITERATURE CITED

- ALEXANDER, R.D. & R. S. BIGELOW. 1960. Allochronic speciation in field crickets, and a new species *Acheta veletis*. *Evolution*, 14: 334-346.
- COYNE, J.A. & H. A. ORR. 2004. *Speciation*. Sinauer Associates, Sunderland, Mass.
- FEDER, J.L., S.B. OPP, B. WLAZIO, K. REYNOLDS, W. GO & S. SPISAK. 1994. Host fidelity is an effective premating barrier between sympatric races of the apple maggot fly. *Proc. Natl. Acad. Sci. USA*, 91: 7990-7994.
- FORISTER, M. L. 2005. The influence of host-plant phenology on *Mitoura nelsoni* Boisduval (Lepidoptera: Lycaenidae). *Ann. Entomol. Soc. Am.*, 98: 295-301.
- FORISTER, M.L., J.A. FORDYCE & A.M. SHAPIRO. 2004. Geological barriers and restricted gene flow in the Holarctic skipper *Hesperia comma* (Hesperiidae). *Molecular Ecol.*, 13: 3489-3499.
- GERVAIS, B.R. & A.M. SHAPIRO. 1999. Distribution of edaphic-endemic butterflies in the Sierra Nevada of California. *Global Ecol. and Biogeog.*, 8: 151-162.
- HARRISON, R.G. & S.M. BOGDANOWICZ. 1995. Mitochondrial DNA phylogeny of North American field crickets: Perspectives on the evolution of life-cycles, songs, and habitat associations. *J. Evol. Biol.*, 8: 209-232.
- HUANG, Y., G. ORTI, M. SUTHERLIN, A. DUHACHEK & A ZERA. 2000. Phylogenetic relationships of North American field crickets inferred from mitochondrial DNA data. *Mol. Phylogenet. Evol.*, 17: 48-57.
- MCGUIRE, W.W. 1998. Description of three new subspecies of *Hesperia* (Lepidoptera: Hesperiidae) from the western United States. pp. 461-474 in T.C. Emmel, ed., *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Fla.
- NICE, C.C. & A.M. SHAPIRO. 2001. Population genetic evidence of restricted gene flow between host races in the butterfly genus *Mitoura* (Lycaenidae). *Ann. Entomol. Soc. Amer.*, 94: 257-267.
- PETERSON, M.A. 1995. Phenological isolation, gene flow and developmental differences among low- and high-elevation populations of *Euphilotes enoptes* (Lepidoptera: Lycaenidae). *Evolution*, 49: 446-455.
- PRATT, G.F. 1994. Evolution of *Euphilotes* (Lepidoptera: Lycaenidae) by seasonal and host shifts. *Biol. J. Linn. Soc.*, 51: 387-416.
- PRATT, G.F. & G.R. BALMER. 1991. Three biotypes of *Apodemia mormo* (Riodinidae) in the Mojave Desert. *J. Lepid. Soc.*, 45: 46-57.
- PRATT, G.F. & J.F. EMMEL. 1998. Revision of the *Euphilotes enoptes* and *E. battoides* complexes (Lycaenidae). pp. 207-270 in T.C. Emmel, ed., *Systematics of Western North American Butterflies*. Mariposa Press, Gainesville, Fla.
- SCOTT, J.A. 1998. New western North American butterflies. *Papilio (N.S.)*, 11: 1-12.
- SHAPIRO, A.M. 1991. Significant additions to the butterflies of the Trinity Alps and Mount Eddy, Northern California. *J. Res. Lepid.*, 29: 33-36.
- SHAPIRO, A.M., C.A. PALM & K.L. WCISLO. 1981. The ecology and biogeography of the butterflies of the Trinity Alps and Mount Eddy, Northern California. *J. Res. Lepid.*, 18: 69-152.

HESPERIA LINDSEYI MCCORKLEI (HESPERIIDAE): A NEW SUBSPECIES OF SKIPPER FROM SOUTHWESTERN OREGON, USA

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ABSTRACT. A new subspecies of *Hesperia lindseyi* Holland is described from southwestern Oregon, United States. This subspecies, *Hesperia lindseyi mccorklei*, is the northernmost known taxon of the *Hesperia lindseyi* group, which is mostly distributed throughout Californian savanna and chaparral plant communities. *H. l. mccorklei* presently appears to be isolated to the Jackson Creek and South Umpqua River drainages in Douglas County, Oregon.

Additional key words: skippers, oak savanna, chaparral

Hesperia lindseyi (Holland, 1930) HesperIIDae is a taxon that occupies various grasslands, chaparral, and savanna habitats of California, with outlying populations in southern Oregon and northwestern Nevada (MacNeill 1964, Dornfeld 1980, Hinchliff 1994, Pyle 2002). Recently, Emmel *et al.* (1998) designated three new subspecies of *Hesperia lindseyi* based on geographically distinct phenotypes that were originally delimited by MacNeill (1964). *Hesperia lindseyi macneilli* Emmel, Emmel and Mattoon, 1998 occurs from coastal southern Marin Co., California north to southern Humboldt County and was considered the darkest of the *H. lindseyi* subspecies. *H. l. eldorado* Emmel, Emmel, and Mattoon, 1998 inhabits the western foothills of the Sierra Nevada from its most southern distribution in El Dorado Co., California north to Butte County. The third subspecific taxon described, *H. l. septentrionalis* Emmel, Emmel and Mattoon, 1998 occupies the northernmost latitudes of the three *H. lindseyi* subspecies. It occurs from low to middle elevations in the Siskiyou Mountains in northern California and southwestern Oregon, and extends eastward across the Klamath Basin of south-central Oregon into northwestern Nevada. The immature stages of *Hesperia lindseyi* consume grasses, primarily *Festuca idahoensis* and *Danthonia californica* Boland Poaceae (MacNeill 1964, 1975). These grasses are generally shade intolerant and are commonly encountered in drier, mesic grasslands, scrub, savanna and chaparral plant communities (Hitchcock 1970).

In Oregon, *Hesperia lindseyi septentrionalis*, is confined to the southern portion of the state. It is commonly taken by collectors in oak (*Quercus kelloggii* Newb. and *Q. garryana* Dougl. ex Hook. Fagaceae) savanna remnants near the Oregon/California border, in

and near the town of Klamath Falls, and occasionally in the Warner Mountains of Lake County (Warren 2005). On 6 June 1996 the northernmost known population of *H. lindseyi* was discovered by Donald G. Severns in southern Douglas County, Oregon, approximately 12 km east of the town of Tiller along Jackson Creek in the South Umpqua River drainage. This population of *H. lindseyi* is approximately 70 km north of the nearest known populations of *H. lindseyi septentrionalis*, is phenotypically distinct, and exists in an isolated remnant of oak savanna surrounded by Douglas fir (*Pseudotsuga menziesii* Mirbel Franco Pinaceae) forests. In the following pages we describe a new subspecies of *Hesperia lindseyi*, comment on its life history, and discuss the geographic bounds for the new taxon.

Hesperia lindseyi mccorklei Severns and Severns, new subspecies

Description. Male. Mean forewing width 11.8 mm, ranging from 10.5 to 13.0 mm ($n = 38$). Dorsal surface (Fig. 1): Forewing bright orange and slightly iridescent; outer black margin extends into inner two thirds of forewing, often surrounding and defining the apical and subterminal spots; post-stigmal patch appears larger and darker when compared to all other *Hesperia lindseyi*. Fringe is brownish-buff with the vein terminals marked by the presence of black scales. Hindwing ground color same as forewing; black hindwing margins extend to distal end of the macular arm band. Lighter orange areas correspond with macular band spotting, which tends to contrast with the ground color. Fringe unbroken throughout the hindwing margin, ranging from cream to buff.

Ventral surface (Fig. 1): Pale orange-brown ground color becoming inwardly buff, abruptly transitioning to black near thorax; apical and subterminal spots surrounded by a field of golden-green scales with intermittent melanic scales covering approximately one third of distal forewing. Apical and subterminal spots cream with a slight greenish tinge, area below stigma is black. A black terminal line runs the length of the forewing separating the fringe from the rest of the wing; vein terminals are marked with enlarged areas of black scales extending from terminal line to fringe edge. Hindwing ground color same as area surrounding the ventral forewing apical and



FIG. 1. A). *H. l. mccorklei*, female holotype, dorsal/ventral. Data in text. B). *H. l. mccorklei*, male allotype, dorsal/ventral. Data in text. C). *H. l. septentrionalis*, female, dorsal/ventral "East of O.T.I., Klamath Falls, Klamath Co, OR, 21 June 1996" D. Severns leg. D). *H. l. septentrionalis*, male, dorsal/ventral, capture data same as female. E). *H. l. macneillii*, female, dorsal/ventral "Etsel Ridge el. 4,600 ft, 5 mi. S. Eel River R.S., Mendocino Co. CA, 13-June-1972, J. Shepard" F). *H. l. macneillii*, male, dorsal/ventral, same capture data as female.

subapical spots; macular band cream with a slightly green tinge. Generally, slightly darker greenish cream scales extend along veins that contact the macular band (but light venation may be absent in some individuals). Vanal area orange-buff, occasionally with a greenish tinge and melanic scales near basal areas. Fringe cream and unbroken throughout hindwing.

Female. Mean female forewing width 14.6 mm ranging from 13 to 16 mm ($n = 22$). Dorsal surface (Fig. 1): Forewing ground color dark brown on margins becoming lighter inwardly, grading to tawny near thorax. Subapical spots conspicuously defined by ventral surface ground color, spots generally cream with a light orange hue. Apical spots joined by pale orange areas, approximately equal in size to apical spots, running down the forewing, bounded inwardly by lighter areas resulting in a banded appearance. Forewing fringe light gray, and broken by black scales at vein terminals. Hindwing ground color generally uniform, ranging from dark brown to tawny. Macular spots warm orange-brown and defined by comparably darker ground color. Hindwing fringe light gray, unbroken, extending along entire hindwing.

Ventral surface (Fig. 1): Central forewing occupied by coal-gray scales beginning near thorax, extending to center of forewing. Above

central forewing melanic region, ground color is orange, below melanic region ground color is buff. Apical and subterminal spots cream, surrounded by golden, olive green scales with considerable melanic overscaling, overall appearing golden, forest-green. Fringe light gray; vein terminals black, extending through hindwing terminal line that runs along the entire forewing. Ventral hindwing ground color golden, olive green with frequent melanic scales, overall appearing golden, forest-green. Veins, same as ventral hindwing ground color. Macular band appears nearly white and weakly silvered, sharply contrasting with ventral hindwing ground color. Vanal area orange-buff, with occasional melanic scales inwardly. Fringe light gray, remaining unbroken for length of hindwing.

Types. **Holotype:** ♀ Oregon, Douglas County, Hillside north of Jackson Creek Road, 3.8 miles east of the junction with South Umpqua Road (UTMs: N 4755771 m, E 10 514710 m, 1470 ft elevation), 19 June 2004, leg Paul M. Severns; bearing white printed label with the above information and printed red label reading "*Hesperia lindseyi mccorklei* ♀, P.M. Severns and D.G. Severns 2005". **Allotype:** ♂, same locality as holotype, 19 June 2004, leg Paul M. Severns, bearing white printed label and red printed label like holotype. **Paratypes:** 134 ♂ and 36 ♀ all collected from the same

locality as the holotype. D.G. Severns: 2 ♂ and 1 ♀ on 4 July 1999, 2 ♂ 9 July 1999, 4 ♂ and 3 ♀ on 24 June 2000, 2 ♂ 14 July 2003, 4 ♀ 19 June 2004. Paul M. Severns: 9 ♀ and 5 ♂ on 19 June 2004. Andrew D. Warren: 20 ♂ 14 July 2003, 50 ♂ and 1 ♀ on 17 July 2003, 30 ♂ and 23 ♀ on 27 July 2003.

The holotype and allotype and six male paratypes will be deposited at the McGuire Center for Lepidoptera Research (MCLR), Sarasota, Florida. One female and five male paratypes will be deposited at each of the following institutions: Oregon State Arthropod Collection (OSAC), Corvallis, California Academy of Sciences, San Francisco, and the American Museum of Natural History, New York. One hundred male paratypes and 32 female paratypes are housed in the private collection of Andrew D. Warren, nine male and four female paratypes are held in the private collection of Donald G. Severns, and five female and five male paratypes are in the private collection of Paul M. Severns.

Etymology. We name this species in honor of David V. McCorkle, for his lifetime contribution to our understanding of Pacific Northwest Lepidoptera, his encouragement to amateur lepidopterists, and the many years of organizing the Northwest Lepidopterists' Society annual meetings.

Diagnosis. *Hesperia lindseyi mccorklei* can be readily distinguished from its nearest geographic conspecific taxon, *H. l. septentrionalis*, by an overall darker appearance on both the dorsal and ventral surface of males and females (Fig. 1). Some of the darkest males and females of *H. l. septentrionalis* may morphologically resemble the lightest individuals of *H. l. mccorklei*, but of all the described subspecies of *H. lindseyi*, *H. l. mccorklei* is the darkest (Fig. 1). Furthermore, essentially all females of *H. l. mccorklei* lack white or cream colored scales extending from the macular spots along the veins on the ventral hindwing that gives *H. l. septentrionalis* its "shaggy" appearance (Fig. 1), a diagnostic wing character for the subspecies (Emmel *et al.* 1998). The lack of light colored scales on the female ventral hindwings separates all other subspecific taxa of *H. lindseyi* from *H. l. mccorklei*.

DISCUSSION

H. l. mccorklei is apparently restricted to the Jackson Creek drainage and associated habitat along the South Umpqua River of Douglas County, Oregon. A single female (OSAC) and two males (MCLR) resembling *H. l. mccorklei* were collected by J. Hinchliff on 20 June 1976, bearing the locality of "Jumpoff Joe Creek, Josephine Co., OR". Unfortunately, this population of *H. lindseyi* has not been relocated, perhaps due to the vague locality on the specimen label. Jumpoff Joe Creek runs from the western foothills of the Cascades to the northern edge of the Siskiyou Mountains and roads line the creek along its course. Given the ambiguity of the Jumpoff Joe Creek locality, *H. l. mccorklei* may extend to the northern edge of the Siskiyou Mountains where it would likely blend with *H. l. septentrionalis*, or

skirt along the western edge of the southern Cascades where it may also contact *H. l. septentrionalis*. However, three male *H. lindseyi* (MCLR) collected by S. Jewett on 5 July 1975 near Rough and Ready Creek, Josephine Co., OR (on the north side of the Siskiyou Mountains) appear to be of the phenotype ascribed to *H. l. septentrionalis* (A. Warren personal communication 2004). The phenotype of the Rough and Ready Creek individuals suggest that *H. l. mccorklei* is more likely to occupy the western edge of the southern Cascades foothills, but more exploration is needed to delimit the taxon's distribution.

At the type locality, *H. l. mccorklei* inhabits oak savanna with young *Pinus ponderosa* and *Pseudotsuga menziesii* trees encroaching into the open areas between the scattered oaks. The habitat at the type locality extends at least 3 km upstream on Jackson Creek and also runs approximately 2 km along a low-lying ridge to the north. *H. l. mccorklei* flies from mid June through mid July amongst the small open grassy areas between and beneath large oak trees and pines. Both males and females commonly nectar on the preferred *Prunella vulgaris* L. *Lamiaceae* and *Brodiaea elegans* Hoover *Liliaceae*, but they also perch on and occasionally probe the flowers of *Leucanthemum vulgare* Lam. *Asteraceae* for nectar. When temperatures exceed 23–25° C, females often perch beneath the shade of trees on nectar plants as well as on the inflorescences of numerous grass species. Males patrol open patches of grass in the direct sun, presumably searching for newly eclosed females. We did not directly observe any oviposition events, but one of the known host plants for *Hesperia lindseyi*, *Danthonia californica* Boland. *Poaceae*, is common in the meadows where *H. l. mccorklei* flies. *Danthonia californica* also appears to be in relative proportions to the adult butterfly population, while the other *Festuca* spp. are uncommon and have low relative abundance.

Aside from the suitable habitat around the type locality, potential sites for other populations of *H. l. mccorklei* are scattered 5–10 km up- and downstream of the confluence with Jackson Creek on the South Umpqua River. The oak chaparral habitat is uncommon along the South Umpqua River and is isolated from other suitable savanna habitat to the south and north by 40–50 km wide swaths of dense, Douglas fir forests. Some of these fir forests were historically oak chaparral, but were planted within the last 100 years with Douglas fir trees for logging. Presently, logging practices threaten *H. l. mccorklei* at its type locality as a large portion of the habitat, approximately 40 ha, was bladed of all vegetation and replanted with Douglas fir within the last three years. About a third of the remaining

habitat at the type locality appeared to be flagged for future tree harvest and planted Douglas fir seedlings, as well as natural volunteers, threaten to close the open gaps that support *H. l. mccorklei* larval and nectar plants.

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LITERATURE CITED

- DORNFELD, E. J. 1980. The butterflies of Oregon. Timber Press, Forest Grove, Oregon. 276 pp.
- EMMEL, T. C. (Ed.). 1998. Systematics of western North American butterflies. Mariposa Press, Gainesville, Florida. 878pp.
- EMMEL, J. F., EMMEL, T. C. & S. O. MATTOON. 1998. Three new subspecies of *Hesperia lindseyi* (Lepidoptera: Hesperidae) in California and northwestern Nevada. In Systematics of western North American butterflies, T. C. Emmel (Ed.) pp: 475-480.
- HINCHLIFF, J. 1994. An atlas of Oregon butterflies. Oregon State University Bookstore, Corvallis. 176 pp
- HITCHCOCK, A. S. 1970. Manual of the grasses of the United States 2nd Ed. Vol. 1. Dover Publications, New York. 569 pp.
- MACNEILL, C. D. 1964. The skippers of the genus *Hesperia* in western North America with special reference to California (Lepidoptera: Hesperidae). University of California Publications in Entomology, Vol. 35. University of California Press, Berkeley. 130 pp.
- . 1975. Hesperidae, pp. 423-578. In: Howe, W. H. (editor). Butterflies of North America. Doubleday & Co., Inc., Garden City, New York. 633 pp.
- PYLE, R. M. 2002. The butterflies of Cascadia. Seattle Audubon Society, Washington, USA. 420 pp.
- WARREN, A. D. 2005. Lepidoptera of North America 6. Butterflies of Oregon. Their taxonomy, distribution, and biology. Contributions of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University. 408pp.

LIFE HISTORY OF *PONTIA DAPLIDICE MOOREI* (RÖBER) (LEPIDOPTERA : PIERIDAE) FROM HIMACHAL PRADESH, INDIA

Butterflies are an important component of the overall biodiversity of a region. They occur in a variety of habitats and are of interest to biologists, naturalists, conservationists and entomologists for specific as well as general reasons. Adult butterflies and their early stages have dual economic importance because they are a significant component of the food chain, and are closely associated with different species of plants. The genus *Pontia* Fabricius is distributed over the entire Palaearctic region, including most of Africa, and enters the north-western part of India. Three species are found in India: *P. daplidice* (Linnaeus), *P. glaucanome* Klug and *P. chloridice* (Hübner) (Talbot, 1939). *Pontia daplidice* (Linnaeus) is represented in the Indian region by only one subspecies, *P. d. moorei* (Röber). Mani (1962) reported *P. d. moorei* from Lahaul Valley (4300m).

This study was carried out at Dr. Y.S. Parmar University of Horticulture and Forestry, Nauni (1440m), Solan, Himachal Pradesh, India. Oviposition on the leaves of *Lepidium rudemale* L. (Brassicaceae) was observed in the field. Freshly laid eggs were located and marked, and were observed daily until hatching. Newly hatched larvae were brought to the laboratory along with leaves, and kept in petri dishes/breeding cages. Fresh leaves were provided daily for the developing caterpillars. Observations on the development and habits were recorded. Measurements of head capsule width, and body length and width were made using with an ocular micrometer adapted to a stereomicroscope.

Oviposition behavior: Oviposition was observed from March to September 2002, between 1000 and 1600 hours, on *L. rudemale*, an herbaceous plant about one foot high. Prior to oviposition females fly slowly, quite close to the ground, and spend a good deal of time fluttering about in search of a suitable leaf. Eggs are placed singly on either the dorsal or ventral surface of tender leaves, each deposition taking three to five seconds. Females then fly off to locate another plant.

Egg (Fig. 1): Height 0.87 ± 0.03 mm, width 0.34 ± 0.02 mm ($n = 28$); bottle shaped, upright, base comparatively broader and rounded; sculptured with prominent ridges, furrows and transverse striae; micropyle end narrow with small circular disc; shiny white when freshly laid, orange after one day, then turning blackish before hatching.

Incubation Period and Hatching: The egg incubation period is four days. The young larva emerges after chewing a hole in the micropyle end of the egg, then eats the egg shell. Hatching takes

about 1.2 hours and occurs mainly in the morning.

Larva: Number of instars: 4

First instar (duration = 2 days, Fig. 2). **Head:** Width 0.34 ± 0.02 mm ($n = 26$); black, with well defined, globular ocelli, and small primary setae. **Body:** Length 2.05 ± 0.04 mm, width 0.36 ± 0.04 mm ($n = 26$); pale yellow, distinctly segmented, small primary setae present on all segments; alimentary canal visible as dark green mid-dorsal stripe; entire body speckled with minute black dots, more dense laterally.

Second instar (duration = 2 days). **Head:** Width 0.70 ± 0.02 mm ($n = 22$); brownish-yellow, sparsely covered with moderately long secondary setae. **Body:** Length 4.46 ± 0.07 mm; width 0.83 ± 0.03 mm ($n = 22$); same as above except with greenish tinge between segments, and with mixture of white and black, primary and secondary setae.

Third instar (duration = 3 days, Fig. 3). **Head:** Width 1.73 ± 0.05 mm ($n = 20$); same as above except light green. **Body:** Length 8.30 ± 0.12 mm; width 1.64 ± 0.17 mm ($n = 20$); mid-dorsal stripe gray; dorsal stripes yellow; subdorsal stripes gray; and spiracular stripes yellow. All stripes extend for the full length of the body.

Fourth instar (duration = 4 days, $n = 20$, Fig. 4). Width 2.4 ± 0.05 mm ($n = 20$); creamish, sparsely covered with mixture of moderately long white and black setae; and with two lateral yellow patches. **Body:** Length 23.0 ± 0.47 mm; width 3.3 ± 0.12 mm ($n = 20$); same as above except gray stripes now broader than yellow stripes; spiracles white surrounded with prominent light green border.

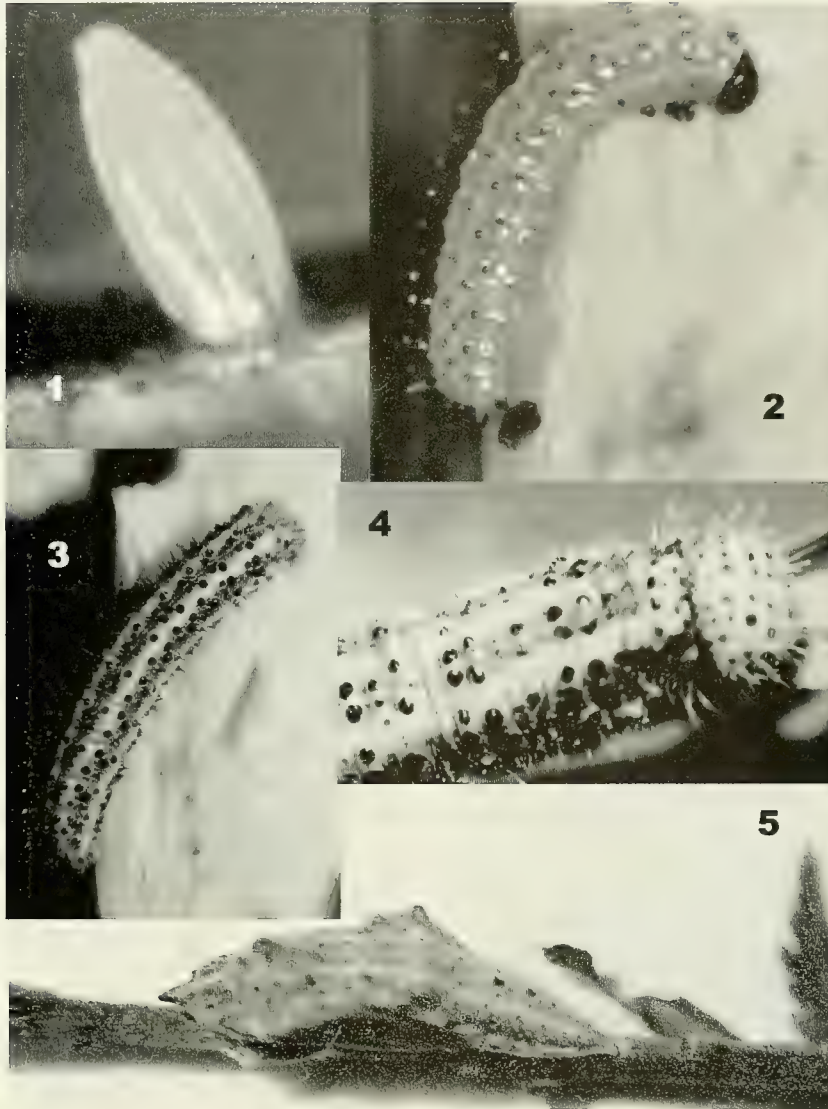
Pupa (duration = 6-7 days, Fig. 5) Length 18 ± 1 mm; width 4.2 ± 0.13 mm; tapering at both ends, with the anterior end drawn out to a spine like point; abdominal segmentation well defined; stripes as in 4th instar except the dorsal stripes now yellowish-green, and the spiracular yellow stripe extends from the posterior end to a point half the body length; spiracles white distinct; entire pupa held closely appressed to the stem or to the ceiling of the breeding chamber, by a well developed silk girdle around the thorax. Pupation took place either on the ceiling of the breeding cage or on the stem of the host plant. Larvae began preparation for pupation at night, and transformed to pupae 10 to 14 hours later.

Adult eclosion is completed within 1.5-2 hours, and usually take place in the morning.

Larval behavior: *Pontia daplidice moorei* is monophagous on *L. rudemale*, and passes through four larval stadia. Each of the three larval ecdyses is completed in 5-9 hours. First instars eat their egg shells, then begin skeletonizing the tender leaves of their host plant, eating the leaf tissue except for the veins. Second instars eat tender leaves except midrib. Third and fourth instars devour the whole leaf including the midrib. First and second instars rest along the midrib on the upper surface of leaf, and third and fourth instars rest either on the stems or on the upper surface of the leaves.

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FIGURES 1-5. *Pontia daplidice moorei*. 1. Egg (ca. 50 \times). 2. First instar (ca. 40 \times). 3. Third instar (ca. 11 \times). 4. Final instar, head and body details (ca. 12 \times). 5. Pupa (ca. 3 \times).

LITERATURE CITED

- MANI, M.S. 1962. Introduction to high altitude Entomology. Methuen and Co. Ltd., London, 302pp.
- TALBOT, G. 1939. The Fauna of British India including Ceylon and Burma. Butterflies ??volume-2. Taylor and Francis, London, 506pp.
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AN EARLY DRAWING OF *CHLOSYNE GORGONE* (HÜBNER) (NYMPHALIDAE) BY JOHN ABBOT

Additional key words. *Chlosyne nycteis*, John Francillon, *Melitaea ismeria*, *Satyrium liparops*

Calhoun (2003, 2004) provided evidence that the enigmatic taxon, *Melitaea ismeria* (Boisduval & Le Conte), is synonymous with *Chlosyne gorgone* (Hübner) rather than *Chlosyne nycteis* (Doubleday) as proposed by Gatrell (1998, 2003). The original description of *M. ismeria* was derived from a drawing of *C. gorgone* by John Abbot (1751-ca. 1840), an English artist-naturalist who lived for many years in Georgia. Abbot sold thousands of illustrations and often duplicated his compositions out of convenience. I subsequently located three other renderings of *C. gorgone* by Abbot and speculated that more may exist (Calhoun 2003). During a recent visit to The Natural History Museum, London, I discovered yet another drawing of the species that offers additional insight into the identity of *M. ismeria*.

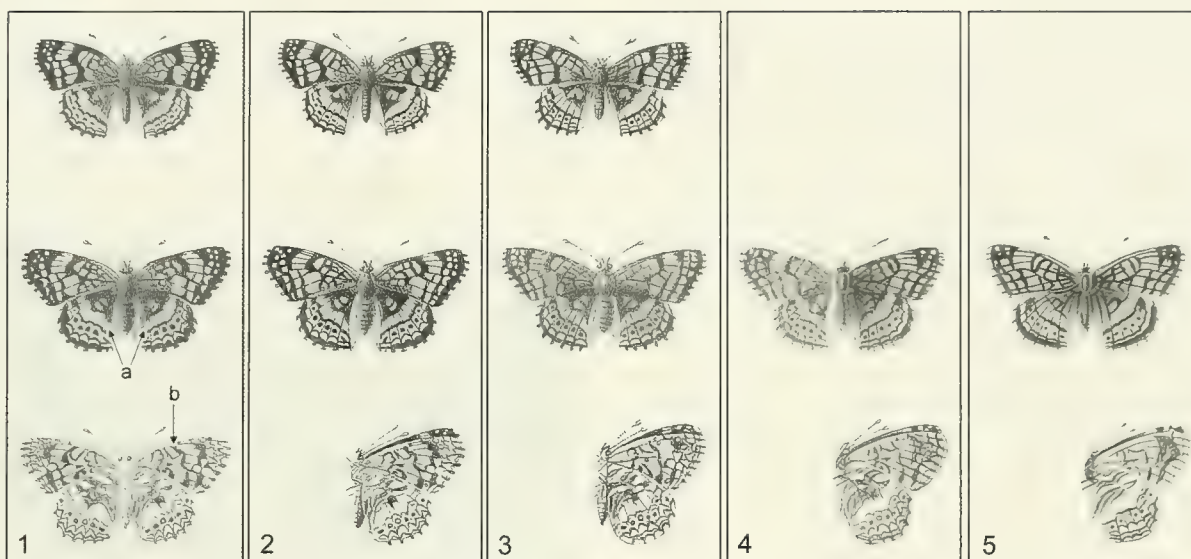
The Natural History Museum contains the largest number of John Abbot's insect watercolors in the world. Most were collected by John Francillon (1744-1816), a London jeweler who acted as Abbot's agent, selling his specimens and drawings to British and European naturalists. Francillon bound his 2,843 invertebrate drawings by Abbot into 17 red morocco volumes. Each drawing is accompanied by manuscript notes that typically include biological information, localities, and common names coined by Abbot. It has been assumed (e.g. Scudder 1872, Harris 1972, Calhoun 2003) that the notes associated with the Lepidoptera drawings were written by Abbot himself. A more thorough analysis confirmed that they were transcribed by Francillon from Abbot's originals. They are consistent with annotations composed by Abbot for his other sets of drawings, but the handwriting matches that of Francillon. Francillon added Latin names, plant identifications, and references to other drawings. He rearranged the drawings into approximate taxonomic order and developed a consistent format for the volumes. A more detailed treatise of the butterfly drawings is planned.

The additional drawing of *C. gorgone* is bound into Francillon's Volume 6 and is rendered in watercolor and graphite in a vertical format. It portrays a dorsal male, dorsal female, and ventral female (Fig. 1). The accompanying notes read, “+++N° 45. *Papilio*, _____. Taken in summer. See N° 7 in Quarto Drawings, Called in Georgia Crosswort Fritillaria.” Francillon left the Latin name incomplete awaiting identification. Drawing “N° 7” is bound into Volume 16 under the heading of “Tab. 7” and portrays *C. gorgone* with immatures and a hostplant (see Calhoun 2003, fig. 3). The common name is apparently Francillon's stylized

version of “Cross wort Fritillary” that Abbot repeatedly used for this species (see Calhoun 2003). Scudder (1872) recorded the drawing in Volume 16, but overlooked the analogous figures in Volume 6.

It is believed that Francillon obtained his invertebrate drawings from Abbot between 1792 and 1812 (Rogers-Price 1997). The engraved title pages for Volumes 6 and 16 are dated 1792 and 1804, respectively. However, this does not necessarily mean that the associated drawings were completed only during those years. The drawings themselves can be useful in determining their chronology. All the ventral butterfly figures in Volume 6 were drawn with fully outstretched wings (Fig. 1), which is consistent with Abbot's earlier works, including the original drawings for Smith & Abbot (1797) that were completed ca. 1783-1792. His later drawings of butterflies (ca. 1800 +) almost always portray ventral adults in more natural poses (Figs. 2-4). This evidence suggests that the drawing of *C. gorgone* in Volume 6 is Abbot's oldest known representation of the species. It was probably rendered at least twenty years prior to his figures for *M. ismeria* (Fig. 4). Abbot reproduced his duplicate figures of *C. gorgone* from the same template illustrations. This is revealed in various subtle characters, such as identical asymmetrical hindwing median bands on the dorsal females (Figs. 1-4). Abbot reproduced only the right half of the ventral adult for his later drawings; a unique wavy black line is present on the forewing of all these figures (Figs. 1-4). For the engraved plate of *M. ismeria* in Boisduval & Le Conte (1829-[1837]), the body of the original dorsal female was altered by another artist to depict a more slender insect. Furthermore, the engraver copied only the right side of this figure for both halves of the corresponding adult on the plate (Figs. 4, 5) (see also Calhoun 2003, 2004).

Abbot's drawings of *Satyrium liparops* (Le Conte) reflect a parallel history. The figures used for the original description of this species were derived from the same set of Abbot drawings as those for *M. ismeria* (Calhoun 2004). Earlier drawings of *S. liparops* are likewise bound into Francillon's Volumes 6 and 16 at The Natural History Museum, London. The adults and immatures in these three drawings are equivalent, but the later figures that were reproduced in Boisduval & Le Conte (1829-[1837]) are less meticulous, resulting in many years of debate about the true identity of the species (see Calhoun 2004, figs. 6, 7). The set of drawings containing the original figures of *S. liparops* and *M. ismeria* were completed by Abbot after he took a brief hiatus, during which he threatened to “quit



FIGS. 1-5. Figures of *C. gorgone* by John Abbot. Top-bottom: dorsal male, dorsal female, ventral female. **1**, From Francillon's Volume 6 (ca. 1792°). Arrows denote shared characters of all the duplicate figures: a, asymmetrical hindwing median bands, b, wavy line on the right ventral forewing. **2**, From Francillon's Volume 16 (ca. 1804°). **3**, For William Swainson (ca. 1816-1818), Alexander Turnbull Library, Wellington, New Zealand; E-272-f-017). **4**, For John E. Le Conte (ca. 1815, Thomas Library, University of South Carolina) (orig. drawing for *M. ismeria*). **5**, From Plate 46 of *M. ismeria* in Boisduval & Le Conte (1829-[1837]). (© The Natural History Museum, London).

Natural history & retire to the Country" (Rogers-Price 1983). These drawings are generally inferior to his other works and it is unfortunate that Boisduval & Le Conte (1829-[1837]) chose them to convey their concepts of several new species. Poorly executed engravings worsened their ambiguity (Fig. 5). Such historical evidence can be invaluable when attempting to determine the status of uncertain taxa.

The newly discovered figures by Abbot are finely delineated and portray *C. gorgone* with more accuracy than any of his subsequent duplicates (Figs. 1-4). In Calhoun (2004) I suggested that his later drawings represent a phenotype tentatively recognized as the multivoltine subspecies *C. g. carlota* (Reakirt). Abbot's more detailed early figures support this identification, as does his associated reference to collecting the species during "summer."

Many thanks to Richard Kielb of the Entomology Library, The Natural History Museum, London, for his kindness and assistance during my visit. Marian Minson (Alexander Turnbull Library, Wellington, New Zealand) provided digital scans of the Abbot drawings in her care and granted permission for their reproduction. Patrick G. Scott (Thomas Cooper Library, University of South Carolina) also allowed access and reproduction of original Abbot drawings. Suzanne Smailes (Thomas Library, Wittenberg University, Springfield, Ohio) supplied scans of plates from Boisduval & Le Conte (1829-[1837]). Manuscript librarians at the British Library (London) compared handwriting samples of J. Francillon. Finally, I thank James K. Adams and Andrew D. Warren for critically reviewing the manuscript.

LITERATURE CITED

BOISDUVAL, J. B. A. D. DE. & J. E. LE CONTE. 1829-[1837]. Histoire générale et iconographie des Lépidoptères et des chenilles de l'Amérique septentrionale. Librairie Encyclopédique de Roret,

Paris. 228 pp., 78 pl.

CALHOUN, J. V. 2003. The history and true identity of *Melittaea ismeria* (Nymphalidae): a remarkable tale of duplication, misinterpretation, and presumption. *J. Lepid. Soc.* 57:204-219.

—. 2004. Histoire générale et iconographie des Lépidoptères et des chenilles de l'Amérique septentrionale by Boisduval & Le Conte (1829-[1837]): original drawings for the engraved plates and the true identities of four figured taxa. *J. Lepid. Soc.* 58:143-168.

GATRELLE, R. R. 1998. The rediscovery, taxonomy, and biology of *Chlosyne gorgone gorgone* and *Chlosyne ismeria* (Nymphalidae) in Burke County, Georgia. *Taxon. Rpt.* 1(2):1-9.

—. 2003. A taxonomic review of *Chlosyne ismeria* with description of a new *ismeria* subspecies from the southern Appalachian Mountains. *Taxon. Rpt.* 4(4):1-15.

HARRIS, L. 1972. The butterflies of Georgia. Univ. Oklahoma Pr., Norman, Oklahoma. 326 pp.

ROGERS-PRICE, V. 1983. John Abbot in Georgia: the vision of a naturalist artist (1751-ca. 1840). Madison-Morgan Cult. Ctr., Madison, Georgia. 149 pp.

—. 1997. John Abbot's birds of Georgia; selected drawings from the Houghton Library, Harvard University. Beehive Pr., Savannah, Georgia. i-xlii, 25 pl.

SCUDDER, S. H. 1872. Abbott's [sic.] notes on Georgian butterflies. *Can. Entomol.* 4:73-77, 84-87.

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A NEW HOSTPLANT RECORD FOR *STRYMON MARTIALIS* (LYCAENIDAE: THECLINAE) IN THE FLORIDA KEYS

Additional Key Words: *Cyclargus thomasi bethunebakeri*, *Caesalpinia bonduc*, *Camponotus*, Fabaceae, competition

Strymon martialis Herrich-Schäffer is a colorful hairstreak widely distributed throughout south Florida, the Bahamas, and western portions of the Greater Antilles (Smith et al. 1994). It is locally abundant on the south Florida mainland and in the Florida Keys. In the Keys it is a maritime species, being primarily restricted to coastal localities including tropical pinelands, hardwood hammock margins, beach dunes, scrubby shorelines, and adjacent open, disturbed sites. Within these habitats, *S. martialis* is found in close association with its only two documented larval hostplants, *Trema micranthum* (L.) Blume (Ulmaceae) and *Suriana maritima* L. (Surianaceae) (Minno & Emmel 1993; Slosson 1901). The developing larvae feed on host flowers, fruits and leaves (Scott 1986).

We regularly encountered the butterfly on many islands within the Lower Florida Keys while conducting status surveys for *Cyclargus thomasi bethunebakeri* (Comstock & Huntington) (Lycaenidae) during 2002 and 2003. The two butterflies fly together in Bahia Honda State Park, sharing much of the available beach dune and coastal strand habitat. *S. maritima* is found commonly across most of Bahia Honda supporting numerous populations of both larval and adult *S. martialis*. We have consistently recorded eggs and developing larvae of *S. martialis* during routine plant examinations.

On 9 March 2003, we observed a female *S. martialis* depositing a single egg on the terminal growth of *Caesalpinia bonduc* (L.) Roxb. (Fabaceae). Although the observation was initially dismissed as an ovipositional error, we repeatedly documented additional eggs on *C. bonduc* during subsequent visits to the park. All were located on new, terminal shoots and flower stalks, and often found adjacent to ova of *C. thomasi bethunebakeri*.

The suitability of *C. bonduc* as a viable larval host was later confirmed on 20 November 2003 when a late instar larva was discovered feeding on a developing flower stalk of a single plant adjacent to the entrance of the Silver Palm Nature Trail on the eastern end of the park. The larva was found in association with individuals of *Camponotus abdominalis floridanus* (Buckley) (Formicidae) (Figure 1) that repeatedly tended the larva and aggressively defended it when



FIGURE 1. Larva of *Strymon martialis* with *Camponotus abdominalis floridanus* ants on a flower stalk of *Caesalpinia bonduc*.

disturbed. Two additional larvae were located on a large patch of *C. bonduc* approximately 5.5 kilometers to the west of Bahia Honda on neighboring West Summerland Key. In this instance, both larvae were in close association with *Camponotus planatus* Roger (Formicidae) while feeding on a developing flower stalk. A single fourth instar larva was collected from the West Summerland Key site and reared in captivity on *C. bonduc* until pupation at our University of Florida laboratory in Gainesville, and a resulting male *S. martialis* eclosed on 21 December 2003.

The selection and use of *C. bonduc* represents a new hostplant record for *S. martialis*, and is the only member of the Fabaceae to be utilized. The additional observed interaction with *Camponotus* ants is the first report of myrmecophily for this abundant South Florida butterfly. Further studies are needed to determine to what extent and frequency *S. martialis* uses *C. bonduc* for oviposition and maturation to the adult in south Florida and the keys. Although eggs were found on both new terminal shoots as well as flower stalks, larvae were only observed feeding on developing flower buds and individual flowers indicating possible nutritional preferences or secondary plant chemical compound limitations.

If *C. bonduc* is selected on a regular basis, additional research is required to determine if such use could potentially lead to competition with *C. thomasi bethunebakeri* for availability of optimal host resources.

Secondarily, such use could disrupt existing ant interaction should workers preferentially tend the larger *S. martialis* larvae over *C. thomasi bethunebakeri* owing to the possibility of a more significant food reward.

LITERATURE CITED

- MINNO, M. C. & T. C. EMMEL. 1993. Butterflies of the Florida Keys. Scientific Publishers Gainesville, Florida. 168 pp.
SCOTT, J. A. 1986. The butterflies of North America. Stanford University Press, Stanford, California. 583 pp.

Journal of the Lepidopterists' Society
59(3). 2005. 175–177

SLOSSON, A. T. 1901. A successful failure. *Entomol. News* 12: 200–203. 236–239.

SMITH, D. S., L. D. MILLER & J. Y. MILLER. 1994. The butterflies of the West Indies and South Florida. Oxford University Press. Oxford. 264 pp.

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NEW LARVAL HOST PLANT FOR *LYCAEIDES MELISSA MELISSA* IN WISCONSIN AND MINNESOTA AND POTENTIAL THREAT TO *LYCAEIDES MELISSA SAMUELIS* (LYCAENIDAE)

Additional key words: Fabaceae, *Coronilla varia*, exotic species

The melissa blue, *Lycaeides melissa* (W. H. Edwards), utilizes a number of plants in the family Fabaceae as larval foodplants, with members of the genera *Astragalus* L. and *Lupinus* L. prominently represented (Scott 1986). The nominate subspecies of this butterfly occurs throughout western Minnesota, most commonly in remnants of the prairie that originally covered that part of the state, where native species of *Astragalus* appear to be the principal hosts. We have records from *A. crassicaarpus* Nutt., *A. adsurgens* Pallas, *A. missouriensis* Nutt., *A. flexuosus* Douglas, and *A. lotiflorus* Hook., as well as from a loco-weed, *Oxytropis lambertii* Pursh., a member of the same tribe in the Fabaceae as *Astragalus* (Gleason & Cronquist 1991). The butterfly is also sometimes found in the same part of the state in association with alfalfa, *Medicago sativa* L., in non-native habitat, e.g., along roadsides, in hayfields, or in pastures, where few prairie species are present (RPD, personal observation). Alfalfa is the principal larval host for some populations of *L. melissa* in western North America (Nice & Shapiro 1999). We report here the discovery of colonies of *L. m. melissa* in western Wisconsin and eastern Minnesota that are using another introduced legume as larval host, crown-vetch, *Coronilla varia* L. The use of this plant does not appear to have been previously reported. This is also the first reported occurrence of the nominate subspecies of *L. melissa* in Wisconsin.

In late July and early August 1994, CL encountered second-brood adults along a short stretch of high-voltage transmission line right of way in St. Croix County, Wisconsin, just northeast of the town of Hudson. Females were observed ovipositing on crown-vetch and on sweet clovers, *Melilotus alba* Medikus and *M. officinalis* (L.) Pallas. Several adults of both sexes

were collected in 1994 and on a subsequent visit on 25 July 2002. Females are typical *L. m. melissa*, with a fully-developed, continuous submarginal orange band on the dorsal forewing as well as the hindwing. Voucher specimens are deposited in the University of Minnesota Insect Collection, University of Minnesota, St. Paul.

RPD revisited the site 6 July and 12 July 2003 and found several second-brood larvae feeding on crown-vetch. All were feeding on leaves except for a probable second instar that was feeding on a very immature developing inflorescence. Early instars feeding on foliage mined out the mesophyll layer, leaving whitened "windowpanes" of epidermal tissue in the leaflets of the pinnately compound leaves. Late instars consumed epidermis as well, stripping most or all the leaflets from a leaf and leaving the rachis studded with the minute leaflet pedicels. These tell-tale signs of larval feeding were more readily found than the larvae themselves. Sweet clover plants were uncommon, and no interactions of females with these were observed. The only other legume noted at this site was round-headed bush-clover, *Lespedeza capitata* Michx., and there was no evidence of use of this plant. Adult activity, except for nectaring, was closely associated with crown-vetch patches. Three larvae were collected from the site on the 12 July visit and reared on potted crown-vetch plants. All developed into adults; two males and a female.

The power line right of way is a former railroad bed that is cut down a few feet below grade in the stretch occupied by the butterfly colony. The soil is a loamy coarse gravelly sand. At the time of the discovery, agricultural fields bordered the site on the north and a windbreak of elm and green ash trees bordered it on the south. The fields have subsequently been converted to

large-lot housing. The corridor itself is dominated by crown-vetch; leafy spurge, *Euphorbia esula* L.; spotted knapweed, *Centaurea maculosa* Lam.; and Canada bluegrass, *Poa compressa* L. Some prairie species such as stiff tickseed, *Coreopsis palmata* Nutt.; rough blazing star, *Liatris aspera* Michx.; Indian grass, *Sorghastrum nutans* (L.) Nash; porcupine grass, *Stipa spartea* Trin.; and little bluestem, *Schizachyrium scoparium* (Michx.) Nash, are present but not common. The crown-vetch-infested stretch of the right of way extends only about 200 meters. CL surveyed about 5 km of the right of way continuing northeast of the colony location in 1994 but encountered no additional occurrences of the butterfly. A search by RPD of about 2 km of this same stretch on 30 July 2002 was similarly unsuccessful. However, on a brief visit on 14 July 2004 RPD found butterflies around the large transformer substation 100 m west of the original location, on the north side of the old railroad. Freshly-emerged second-brood adults were flying about in thin vegetation on the dry, gravelly apron that surrounds the fenced substation. Depauperate crown-vetch plants are common here.

In August 1996 DH discovered another colony of *L. m. melissa* that is using crown-vetch as a larval host, although in this case it is also using ground-plum, *Astragalus crassicaupus* Nutt. This colony is in eastern Minnesota, ca. 4.5 km east of Dennison in Goodhue County. During this and several subsequent visits we have observed butterflies to be common along a ca. 0.7 km stretch of west-facing highway cutbank in weathered limestone and shale where crown-vetch is the major plant cover and in a small remnant of degraded prairie thoroughly invaded by crown-vetch on gentler slopes above part of the cutbank. A few small aggregations of ground-plum plants occur in the prairie remnant. Cultivated fields border the cutbank and prairie remnant on the east. Woods and cultivated fields occupy the small valley on the west side of the road.

On 13 June 2004 RPD observed a female oviposit on the stem of crown-vetch plant at this site, and another oviposit on a grass blade while crawling down a crown-vetch stem. During visits on 26 June and 4 July 2004 RPD found a total of 12 larvae feeding on crown-vetch, most commonly on foliage, but occasionally on flowers. Larvae were discovered by searching for the distinctive behavior of attending ants, a large, dark species of *Formica* L. whose mounds were common. (Attending ants at the Hudson site were small, probably belonging to at least two species). Two of these larvae were collected and reared to pupation on crown-vetch. A braconid wasp emerged from one pupa, a male butterfly from the other.

On the 13 June visit a number of ova and two first-

instar larvae were observed on ground-plum plants, and on the two subsequent visits 12 larvae were observed feeding on ground-plum. Approximately one-third of the ground-plum plants examined had ova, larvae, or "windowpaning" evidence of larval feeding. Count was not kept of the number of searches of crown-vetch plants, but the success rate was probably no greater than one in 20. The compact habit of ground-plum makes finding ova, larvae, and feeding damage on it easier than on the more diffuse crown-vetch plants, but the difference does not seem enough to account for the different success rates; rather, a preference for ground-plum by ovipositing females seems to be indicated. However, the number of ground-plum plants present in this site is too small to have produced the number of *L. m. melissa* adults observed. Crown-vetch thus appears to be the major host plant of this colony.

The adaptation to crown-vetch by *L. m. melissa* is of more than ordinary interest because the widespread establishment of this plant along roadsides in the northeastern U.S. provides ready corridors for this taxon to invade the range of the federally endangered Karner blue, *Lycaeides melissa samuelis* Nabokov. Recent allopatry of these two taxa appears to be based on their traditional host-plant dependencies. Wild blue lupine, *Lupinus perennis* L., the only reported larval host for *L. m. samuelis* (Lane & Weller 1994), grows naturally only in sands and does not occur in the prairie habitat of *L. m. melissa* (Ownbey & Morley 1991). Conversely, none of the *Astragalus* or *Oxytropis* species commonly used by the latter occur in the sand barrens habitat of *Lupinus perennis* (Cochrane & Iltis 2000). Crown-vetch planted along roadsides breaks down this separation. The Goodhue County, MN, colony of *L. m. melissa* is at the edge of the range of *L. m. samuelis*, 85 km north-northwest of a colony of the latter in Winona County, MN. The Hudson, WI, colony of *L. m. melissa* is within the historic range of *L. m. samuelis*, 60 km southeast of the former station of the latter in Anoka County, MN (now extirpated) and 65 km south of the large population in northwest WI. It is also only 65 km west of colonies in Dunn County, WI, that are part of the large central Wisconsin population. This colony represents a clear case of range extension based on adaptation to crown-vetch.

Opportunities for interbreeding that this novel physical proximity would produce could pose a threat to *L. m. samuelis* as a distinct taxon. Because genetic similarity between these taxa is within the range observed between subspecies (Packer et al. 1998; Nice & Shapiro 1999), it is possible that matings between them will produce fully viable offspring. This hybridization could threaten the continued identity of

L. m. samuelis. Such a scenario represents a possibly unrecognized way in which exotic species introductions may affect biodiversity.

The use of alfalfa as a host plant by *L. m. melissa* in western Minnesota has not resulted in an eastward expansion of its range, despite the common occurrence of alfalfa hayfields in the region. The only known occurrence of this taxon associated with alfalfa east of its prairie range in Minnesota is a 1977 record from Morrison County, within the forested region of the state, where RPD encountered a few adults, including both sexes, in an alfalfa hay field (specimens in the University of Minnesota Insect Collection). The present status of the butterfly at this location is not known. It may be that the regular haying of these fields prevents establishment of persistent colonies. Crown-vetch may provide a more suitable basis for range expansion, as most roadside plantings are infrequently mowed. It has supported expansion of another specialized legume-feeder that has adapted to its use, the wild-indigo dusky wing, *Erynnis baptisiae* (Forbes) (Shapiro 1979; Opler 1992). The two locations where we have documented the use of crown-vetch by *L. m. melissa* are droughty habitats where the plants are somewhat stunted and do not form lush, dense mats typical of mesic, fertile sites. If these conditions are important for the successful establishment of this butterfly on crown-vetch, its range expansion may be impeded as such habitats are more discontinuous than the occurrence of crown-vetch itself. However, workers should be on the watch for this butterfly in eastern Minnesota and western Wisconsin.

An effort to determine whether the two taxa will naturally mate, and whether hybrid offspring show any evidence of inviability should be undertaken. If, as we expect will be the case, the two will mate in nature and produce fully viable offspring, eradication of crown-vetch-feeding colonies of *L. m. melissa* may be advisable to protect *L. m. samuelis*. Total eradication of crown-vetch is probably not possible, but reducing it in the vicinity of Karner blue populations would be feasible. The state transportation departments in both Minnesota and Wisconsin have removed crown-vetch from their seed mixes, but many counties and townships in these states continue to plant it (Gary Birch, WI DOT, and Larry Puchalski, MN DOT, personal communication). These entities should be encouraged to discontinue planting crown-vetch in the vicinity of Karner blue populations.

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reviewers; their suggestions much improved the paper.

LITERATURE CITED

- COCHRANE, T. S., & H. H. ILLIS. 2000. Atlas of the Wisconsin prairie and savanna flora. Tech. Bull. No. 191. Wisconsin Dept. of Natural Resources, Madison, WI.
- GLEASON, H. A., & A. CRONQUIST. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd ed. New York Botanical Garden, Bronx, NY. 910 pp.
- LANE, C. P., & S. J. WELLER. 1994. A review of *Lycaeides* Hübner and Karner Blue taxonomy, pp. 5-21. In Andow, D. A., R. J. Baker, & C. P. Lane (eds.), Karner Blue butterfly: a symbol of a vanishing landscape. Misc. pub. 84-1994. Minnesota Agricultural Experiment Station, University of Minnesota. St. Paul, MN.
- NICE, C. C., & A. M. SHAPIRO. 1999. Molecular and morphological divergence in the butterfly genus *Lycaeides* (Lepidoptera: Lycaenidae) in North America: evidence of recent speciation. J. Evol. Biol. 12:936-950.
- OPLER, P. A. 1992. A field guide to eastern butterflies. Houghton Mifflin Co., New York, NY. 396 pp.
- OWNBEY, G. B., & T. MORLEY. 1991. Vascular plants of Minnesota: a checklist and atlas. University of Minnesota Press, Minneapolis, MN. 307 pp.
- PACKER, L., J. S. TAYLOR, D. A. SAVIGNANO, C. A. BLESER, C. P. LANE, & L. A. SOMMERS. 1998. Population biology of an endangered butterfly, *Lycaeides melissa samuelis* (Lepidoptera: Lycaenidae): genetic variation, gene flow, and taxonomic status. Can. J. Zool. 76:320-329.
- SCOTT, J. A. 1986. The butterflies of North America: a natural history and field guide. Stanford University Press, Stanford, CA. 583 pp.
- SHAPIRO, A. M. 1979. *Erynnis baptisiae* (Hesperiidae) on crown vetch (Leguminosae). J. Lepid. Soc. 33:258.

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STANLEY SWENSON NICOLAY

Colonel Stan Nicolay (USMC Retired, Fig. 1), a charter member of the Lepidopterists' Society, died at age 87 on 5 December 2004 at his home in Virginia Beach, VA, USA after a 20 year battle with prostate cancer. Stan contributed prodigiously to the Lepidoptera community and to knowledge of Lepidoptera. He served the Society as President and Treasurer, attended annual meetings regularly for decades, helped establish The Butterfly Society of Virginia, was an active collector in the Neotropics and a superb preparator, had a long association with the Smithsonian Institution (Washington, DC, USA) and the Allyn Museum of Entomology (now part of the McGuire Center for Lepidoptera, Gainesville, FL, USA), and published numerous taxonomic papers on the Neotropical Hesperidae and Lycaenidae.

Stan was born in Colfax, Washington, USA, on 14 March 1917 and began collecting butterflies at age 14. He received a BS degree in Zoology from the University of Washington. Stan considered a career as a professional biologist (his major professor hoped that he would become a Coleopterist), but joined the Marine Corps and became a Marine aviator in 1941. He flew fighter planes in the Pacific in WWII, rising through the ranks during service in the Korean and Vietnam wars to retire as a Marine Corps Colonel in 1968.

Even during his military career, Stan found time for butterflies. For example, in the midst of conflict on Guadalcanal on 18 September 1942, he wrote in his diary, "Had the late patrol today, so had most of the day to myself for a change. Sure collected some nice insects." While stationed later in southern California, he met John Comstock and Lloyd Martin at the Los Angeles County Museum, and they encouraged his interest in Lepidoptera. In 1960 while commanding the military group at Vieques, a small island off the coast of Puerto Rico, he used a lull in military activities to collect butterflies on the island.

Stan's collecting friend, Gordon B. Small, Jr., began a job teaching mathematics in the Canal Zone (now Canal Area) of Panama in September 1962. A few months later, Stan visited Gordon in Panama. It was the first of many collecting trips to the Neotropics, and it solidified Stan's interest in Neotropical Hesperidae and Lycaenidae. In January 1969, Stan flew from Panama to Colombia on a Smithsonian sponsored trip (Fig. 2), which was followed by a jaunt with his son Stephen to Ecuador in 1972. Stan continued to make regular collecting forays to Central and South America

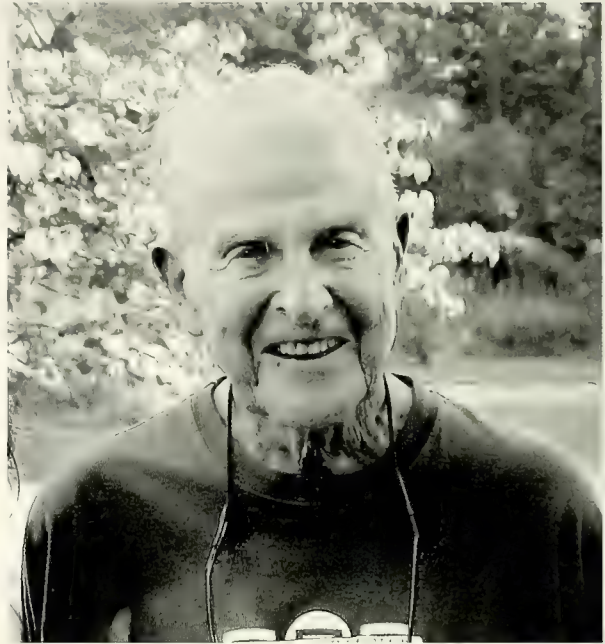


FIGURE 1. Stanley S. Nicolay, July 2004, Virginia Beach, Virginia.

(including Venezuela, Peru, and Brazil) for the next 25 years with a variety of colleagues, including the authors of this obituary. Perhaps the two most significant field trips were a sojourn through the central plateau of Brazil with Keith Brown, Jr., in 1969 and a 3,000 mile journey with Curtis Callaghan in 1978 from Brazil's Rio de Janeiro to Santarem and back on the Transamazonica road system that had just been built. To our knowledge, Stan was the first resident North American butterfly collector to make regular collecting trips to Panama and South America.

Stan was a meticulous "technician." His spreading technique for delicate butterflies used pinning blocks with two fine threads to flatten the wings long enough to apply glassine strips. He was a master at clipping the strong thoracic muscles of skippers to make the wings lie flat. He always intended his collection to be both scientific and aesthetic, and it was. Despite the significant contributions of his scientific papers, he often commented in later years that it was the collecting and technical preparation of specimens that he most enjoyed.

Stan found that he was unable to identify many of the Neotropical Lycaenidae that he had collected and decided in the mid-1960s to write taxonomic papers to help solve this problem. Because he lacked the necessary background, he relied heavily on advice from

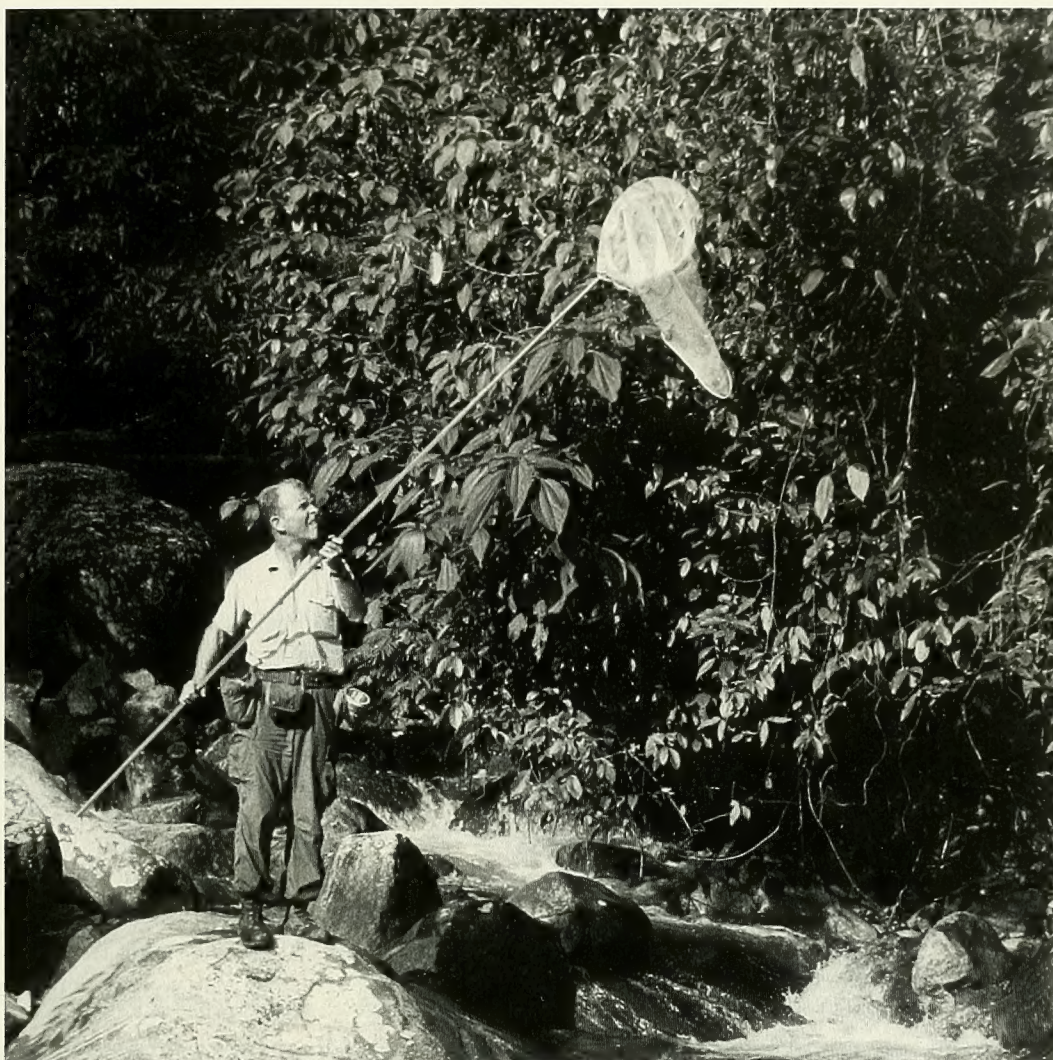


FIGURE 2. Stanley S. Nicolay, 1969, collecting in Caquetá Province, Colombia.

professional biologists, especially Jerry Powell, who was then Editor of the Society's *Journal*. It took him more than five years to write and publish the first paper naming the genus *Symbiopsis*, but other publications followed more quickly. Stan's revisions of lycaenid genera were the first comprehensive works on the Neotropical lycaenid genera and the first to make extensive use of female genitalic morphology (except for two papers by W. D. Field).

Stan's association with the Smithsonian Institution began in 1951 when he met J. F. Gates ("Jack") Clarke, who remained a close friend for almost 40 years. Stan and Gordon Small decided in 1983 to deposit their collections jointly at the Smithsonian's National Museum of Natural History. At the time, their collection consisted of 42,500 pinned specimens, virtually all from the New World (Robbins & Clarke, 1986, *J. Lepid. Soc.* 40:106). Subsequent collecting and

extensive preparation of papered material has increased this donation to about 100,000 specimens.

Stan also had a close friendship with Arthur Allyn that began in the late 1960s when the Allyn Museum was housed in Chicago, Illinois, USA. For many years after the Allyn Museum moved to Sarasota (Florida, USA), Stan spent 2-3 weeks a year working on taxonomic papers with help from Art Allyn, Lee Miller, and Jackie Miller.

Stan was a charter member of the Lepidopterists' Society and was an active participant at annual meetings through 2004. He served as President in 1976, but perhaps his greatest contribution to the Society was as Treasurer (1969-1974). The Society was financially insolvent in 1969 because the Treasurer at that time had been "unable to function." Stan put the books in order and frankly told the Executive Council that there was an immediate shortfall of about \$1,500. He proposed

several remedies: raise dues, pursue paying memberships, and terminate foreign courtesy memberships. These measures were adopted at the 1971 meeting in Louisville, Kentucky, USA, and the late Arthur Allyn gave the Society \$1,500 to solve the immediate deficit. The Society has been solvent ever since.

Stan was active in the formation of The Butterfly Society of Virginia in 1992. This Society is primarily an organization of enthusiasts, and Stan served in a variety of capacities, most notably being an advisor and bringing in outside speakers.

One genus and seven species were named for Stan Nicolay. Patronyms in the Lycaenidae are *Nicolaea* Johnson 1990, *Calycopis nicolayi* Field 1967, *Strymon nicolayi* Johnson, Eisele, & MacPherson 1990, and *Arcas nicolayi* Salazar, & Constantino 1995. Patronyms in other families are *Aguna nicolayi* Austin & Mielke 1998 (Hesperiidae), *Napeogenes achaea nicolayi* Fox & Real 1971 (Nymphalidae), *Charis nicolayi* Hall & Harvey 2001 (Riodinidae), and *Calydna nicolayi* Hall 2002 (Riodinidae).

The skills that enabled Stan to survive as a Marine aviator included an innate ability to navigate and superb eyesight, both particularly valuable skills for a collector in a tropical rain forest. He had a strong sense of his ability to survive in adverse circumstances, which allowed him to make trips to the most remote parts of Latin America, always carrying a net.

Stan was a man of many passions. Besides the Marine Corps and various aspects of lepidopterology, he was active in orchid and bee-keeping organizations. He was a gifted teacher with a strong desire to share his knowledge, whether in the field or giving unrehearsed talks to schoolchildren. Perhaps his greatest passion, however, was as a story teller. Anyone who visited his home, accompanied him on a collecting trip, spent time with him at an annual meeting, or shared a meal of pollo a la brasa and beer was regaled by stories told with compassion, enthusiasm, a point-of-view, and humor. And if Stan liked something, it earned his trademark "Outstanding." It is this "human" side of Stan Nicolay that we will miss most.

Stan is survived by Lilian D. Nicolay, his wife of 62 years, sons Stephen C. and Joseph J. Nicolay, daughter-in-law Dawn Nicolay, and four grandchildren. We are grateful to Joe and Dawn for their kind and generous help in compiling information.

Scientific Publications of S. S. Nicolay

Nicolay, S. S. & G. B. Small, Jr. 1969. A new subspecies of *Pyrrhopyge creon* (Hesperiidae) from Panama. *Journal of the Lepidopterists' Society* 23(2): 127-130, 3 figs.

Nicolay, S. S. 1971a. A new genus of hairstreak from Central and

South America (Lycaenidae, Theclinae). *Journal of the Lepidopterists' Society* 25(Suppl. 1): 1-39, 4 pls., 11 figs.

Nicolay, S. S. 1971b. A review of the genus *Arcas* with descriptions of new species (Lycaenidae, Strymonini). *Journal of the Lepidopterists' Society* 25(2): 87-108, 11 figs. 1971c.

Miller, L. D. & S. S. Nicolay. 1971c. Two new Charaxinae from Panama and the Canal Zone (Nymphalidae). *Bulletin of the Allyn Museum* 1: 1-5, 2 pls., 2 figs.

Nicolay, S. S. 1973. Descriptions of new Neotropical Hesperidae. *Journal of the Lepidopterists' Society* 27(4): 243-257, 35 figs.

Nicolay, S. S. 1975. Illustrations and descriptions of some Pyrrhopyginae from Panama (Hesperiidae). *Journal of Research on the Lepidoptera* 13(3): 181-190, 9 figs.

Nicolay, S. S. 1976. A review of the Hubnerian genera *Panthiades* and *Cycnus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum* 35: 1-30, 25 figs.

Nicolay, S. S. 1977. Studies in the genera of American hairstreaks. 4. A new genus of hairstreak from Central and South America (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum* 44: 1-24, 20 figs.

Nicolay, S. S. 1979. Studies in the genera of American hairstreaks. 5. A review of the Hubnerian genus *Parrhasius* and description of a new genus *Michaelus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum* 56: 1-51, 45 figs.

Nicolay, S. S. 1980a. The genus *Chlorostymon* and a new subspecies of *C. simaethis*. *Journal of the Lepidopterists' Society* 34(2): 253-256, 3 figs.

Nicolay, S. S. 1980b. Descriptions of new Hesperidae from Panama and Ecuador (Pyrginae and Hesperinae). *Bulletin of the Allyn Museum* 59: 1-17, 17 figs.

Nicolay, S. S. & G. B. Small, Jr. 1981. Illustrations and descriptions of some species of Pyrrhopyginae from Costa Rica, Panama and Colombia. *Journal of Research on the Lepidoptera* 19(4): 230-239, 4 figs.

Nicolay, S. S. 1982. Studies in the genera of American hairstreaks. 6. A review of the Hubnerian genus *Olynthus* (Lycaenidae: Eumaeini). *Bulletin of the Allyn Museum* 74: 1-30, 34 figs.

Robbins, R. K. & S. S. Nicolay. 1999a. Taxonomy and nomenclature of *Strymon istapa* and *S. columella* (Lycaenidae: Theclinae: Eumaeini). *Journal of the Lepidopterists' Society* 52(3): 318-327, 16 figs.

Robbins, R. K. & S. S. Nicolay. 1999b. Taxonomy of *Strymon toussainti*, *S. andrewi*, *S. amonensis*, and *S. rhapsos* (Lycaenidae: Theclinae). *Journal of the Lepidopterists' Society* 52(3): 328-334, 14 figs.

Nicolay, S. S. 2000. Book Review of *Revista de Theclinae Colombianos/Review of Colombian Theclinae*. 1997. *Journal of the Lepidopterists' Society* 54(2): 76.

Robbins, R. K. & S. S. Nicolay. 2002. An overview of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini). *Journal of the Lepidopterists' Society* 55(3): 85-100.

Nicolay, S. S. & R. K. Robbins. 2005. Five new dry-area South American *Strymon* species (Lycaenidae: Theclinae) and their biogeographic significance. *Journal of Research on the Lepidoptera* 38: 35-49.

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